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A BIOECOLOGICAL INVESTIGATION IN THE YELLOW DUNE REGION OF TERSCHELLING

BY

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I. FAUNA

Many ecologists have made studies of various types of communities from faunistic and environmental points of view. As it is our aim to combine fauna and vegetational environment into one study, we have chosen a fairly simple community, i.e., the yellow dune region of the Isle of Terschelling, West Frisian Isles, the Netherlands.

The working ground was situated in the nature reserve "De Boschplaat", an area mainly consisting of an extensive duneland, relieved by sandy stretches and salt marshes. It is, for the greater part, unspoiled by human agency. Sea and

wind alone hold this vast territory of ca. 45 km² which has a grandeur, unique in present day western Europe.

Investigations were carried out during three successive years (1950, 1951, and 1952) in a transect, starting in the low fore dunes and stretching 150 m inland across the main dune ridge.

We are indebted to the Foundation of Duneland Research, which offered us hospitality in the Biological Station "Schellingerland" (Plate 25).

Preceding the results of the biocenological investigation, a full record of all specimens collected will be given which may be of interest for the knowledge of the fauna of this part of the Netherlands (Table I).

Previous investigations into the insect fauna of Terschelling have been effected by MACGILLAVRY (1914), KABOS (1942), GEYSKES & DOEKSEN (1949) and GRAVESTEIN (1955). They concern incidental collecting trips, when random samples were taken in places which were likely to be suitable for insects to live in reasonable numbers.

In Table Ia a synopsis is given of the numbers of classes, orders, families, species and individuals collected. These totals are the result of an addition of the numbers captured during each year's investigation.

As may be seen in the table, the Coleoptera make the most numerous order, as regards the family and species content, the Homoptera however, hold the biggest number of individuals.

It is interesting to note that KABOS (l.c.) and GEYSKES & DOEKSEN (l.c.) state that "in coastal regions no other insect order comes into prominence in such way as the Diptera do". In our opinion, this statement is prejudiced, the effect merely being caused by their sampling method (which was especially directed on Diptera). On the other hand, our technique was unfit for sampling flying insects, and we are certain that our results are biased because of this. For example, we were unable to collect the few bumblebees (*Bombus* or *Psithyrus* spec.) and butterflies (*Pieris* spec.) which were flying across the transect; and as we did not find nesting sites or caterpillars, their presence must be considered to be incidental.

In 1951 an invasion of *Talitrus saltator* (Amphipoda) probably coming from the beach, took place in no. 1 sampling area (resp. 72, 22, 53 and 21 individuals in each square). Neither in 1950 nor in 1952 this species was found in the transect.

It is a remarkable fact, that nearly all animals of the macrofauna collected are arthropods. An exception is a specimen of *Vitrina pellucida* (Gastropoda, Pulmonata), collected in 1951 in the *Hippophae*-phase.



Platet 24. In the low fore dunes the sands are frequently subjected to removal and addition by strong on-shore wind

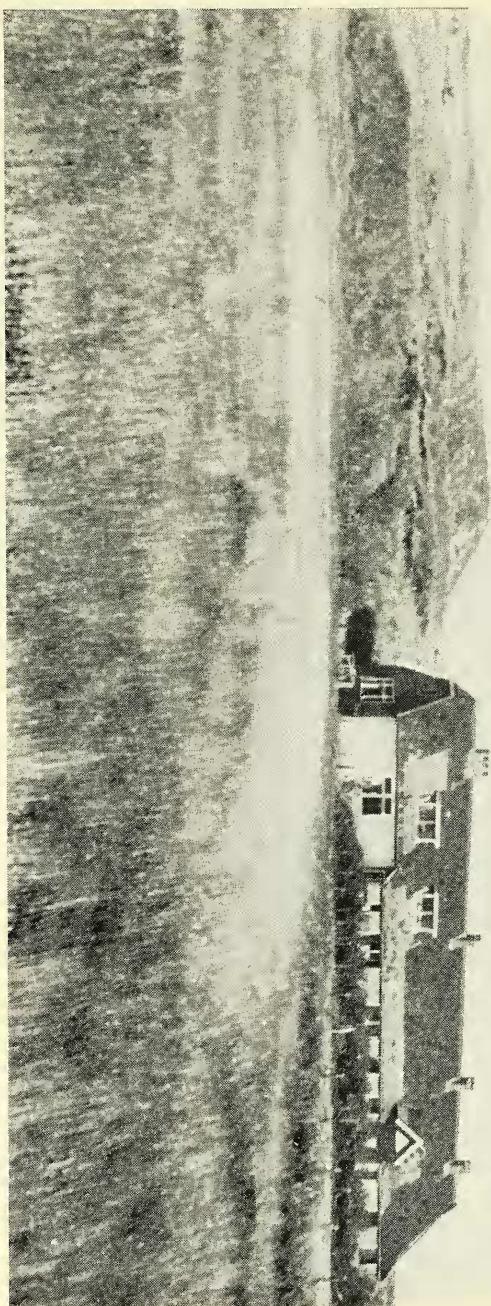


Plate 25. Biological station "Schellingerland" in the West Frisian island of Terschelling
P. F. VAN HERDT & M. F. MÖRZER BRUYN: *Investigation of Terschelling*

Table I. Total numbers of Arthropods, collected in the yellow dune range of the isle of Terschelling. 1—14 August 1950—1951—1952

Family and species	Sample plot analysis no. (S.P.A. no.)								
	1	2	3	4	5	6	7	8	tot.
COLEOPTERA									
Cicindelidae									
<i>Cicindela maritima</i> Latr. (ad. + 1.)	3+1	3	—	—	—	—	—	—	7
Carabidae									
<i>Trechus IV-striatus</i> Schr.	4	44	109	37	32	14	12	16	268
<i>Broscus cephalotes</i> L. (ad. + 1.)	2	5	2	5+3	3+2	9	4+1	—	36
<i>Demetrias monostigma</i> Sam.	1	33	33	161	116	41	6	1	392
(ad. + 1.)	—	+2	+3	+14	+10	+5	—	—	+34
<i>Amara silvicola</i> Zimm.	1	—	1	3	4	18	—	—	27
<i>Bembidion normannum</i> Dej.	—	3	1	—	—	—	—	—	4
<i>Calathus erratus</i> Sahlb.	—	2	1	19	39	95	106	41	303
<i>Harpalus neglectus</i> Dej.	—	1	1	6	73	174	111	68	434
<i>Amara familiaris</i> Dfts.	—	1	—	—	—	—	—	6	7
<i>Dichirotrichus pubescens</i> Payk.	—	1	—	—	—	—	—	—	1
<i>Bradycellus harpalinus</i> Serv.	—	—	2	—	2	—	—	—	4
<i>Calathus melanocephalus</i> L.	—	—	1	1	10	11	2	17	42
<i>Amara spreta</i> Dej.	—	—	—	24	15	8	18	3	68
<i>Calathus mollis</i> Marsh.	—	—	—	19	51	37	95	107	309
<i>Dromius linearis</i> Oliv.	—	—	—	7	27	31	24	8	97
<i>Harpalus servus</i> Dfts. (ad.+1.)	—	—	—	1	9	21	11	7	53
<i>Asaphidion pallipes</i> Dfts.	—	—	—	1	2	—	1	—	4
<i>Dromius melanocephalus</i> Dej.	—	—	—	—	2	—	1	1	4
<i>Amara bifrons</i> Gyll.	—	—	—	—	—	1	—	—	1
<i>Agonum marginatum</i> L.	—	—	—	—	—	1	—	—	1
<i>Amara lucida</i> Dfts.	—	—	—	—	—	—	6	7	13
<i>Metabletus foveatus</i> Geoffr.	—	—	—	—	—	—	4	7	11
<i>Notiophilus aquaticus</i> L.	—	—	—	—	—	—	1	—	1
<i>Notiophilus hypocrita</i> Putz.	—	—	—	—	—	—	1	—	1
<i>Amara aenea</i> DeG.	—	—	—	—	—	—	1	—	1
<i>Amara famelica</i> Zimm.	—	—	—	—	—	—	1	—	1
Staphylinidae									
<i>Aleochara bipustulata</i> Grav.	6	5	15	11	—	1	—	—	38
<i>Philonthus quisquiliarius</i> Gyll.	2	1	—	—	—	—	—	—	3
<i>Tachyporus hypnorum</i> F.	1	4	—	1	4	2	2	1	15
<i>Quedius pallipes</i> Luc.	—	1	—	—	—	—	—	2	3
<i>Philonthus nigritulus</i> Grav.	—	74	15	3	1	1	—	1	95
<i>Aleochara lanuginosa</i> Grav.	—	13	1	2	—	2	2	1	20
<i>Oxytelus tetracarinatus</i> Bl.	—	3	3	2	—	1	—	—	9
<i>Tachinus rufipes</i> DeG.	—	3	—	—	—	1	—	—	4
<i>Aleochara morion</i> Grav.	—	3	—	—	—	—	—	—	3
<i>Oxytelus inustus</i> Grav.	—	2	1	—	—	1	—	—	4
<i>Tachyporus pusillus</i> Grav.	—	2	—	—	—	1	—	—	3
<i>Bledius arenarius</i> Payk.	—	2	—	—	—	—	—	—	2
<i>Stenus melanopus</i> Marsh.	—	2	—	—	—	—	—	—	2
<i>Conurus pedicularius</i> Grav.	—	1	1	2	1	—	3	1	9
<i>Leptacinus batychrus</i> Gyll.	—	1	—	—	—	—	—	1	2
<i>Aleochara verna</i> Say.	—	1	—	—	—	—	—	—	1

Family and species	S.P.A. no.	1	2	3	4	5	6	7	8	tot.
<i>Megarthrus depressus</i> Payk. . . .		—	1	—	—	—	—	—	—	1
<i>Tachyporus chrysomelinus</i> L. . . .		—	1	—	—	—	—	—	—	1
<i>Cardiola obscura</i> Grav.		—	1	—	—	—	—	—	—	1
<i>Micropeplus porcatus</i> F.		—	1	—	—	—	—	—	—	1
<i>Aleochara obscurella</i> Grav.		—	1	—	—	—	—	—	—	1
<i>Platystethus nigens</i> Sahlb.		—	1	—	—	—	—	—	—	1
<i>Philonthus fuscipennis</i> Mnnh. . . .		—	—	14	4	2	2	—	—	22
<i>Tachyporus nitidulus</i> F.		—	—	5	4	—	1	—	—	10
<i>Philonthus varius</i> Gyll.		—	—	3	1	—	—	—	—	4
<i>Aleochara grisea</i> Kr.		—	—	3	—	—	—	—	—	3
<i>Bledius opacus</i> Bl.		—	—	1	2	6	17	2	1	29
<i>Philonthus longicornis</i> St.		—	—	1	—	—	1	—	—	2
<i>Stiliclus orbiculatus</i> Payk.		—	—	1	—	—	—	—	—	1
<i>Platystethus alutaceus</i> Th.		—	—	1	—	—	—	—	—	1
<i>Aleochara inconspicua</i> Aubé		—	—	1	—	—	—	—	—	1
<i>Philonthus laminatus</i> Cr.		—	—	1	—	—	—	—	—	1
<i>Philonthus cruentatus</i> Gmelin. . . .		—	—	—	2	—	—	—	—	2
<i>Philonthus sordidus</i> Grav.		—	—	—	1	—	—	—	—	1
<i>Xantholinus subrufus</i> Reitt.		—	—	—	1	—	—	—	—	1
<i>Stenus providus</i> Er.		—	—	—	—	2	—	—	—	2
<i>Xantholinus angustatus</i> St.		—	—	—	—	1	—	—	—	1
<i>Staphylinus ater</i> Grav.		—	—	—	—	1	—	—	—	1
<i>Tachyporus solitus</i> Er.		—	—	—	—	1	—	—	—	1
<i>Astilbus canaliculatus</i> F. (ad.+l.)		—	—	—	—	—	4	16	+2	34
<i>Xantholinus linearis</i> Ol.		—	—	—	—	—	1	1	4	6
<i>Quedius boops</i> Grav.		—	—	—	—	—	—	—	—	3
<i>Stenus clavigornis</i> Scop.		—	—	—	—	—	—	—	—	2
<i>Quedius tristis</i> Grav.		—	—	—	—	—	—	—	—	1
<i>Quedius picipes</i> Mnnh.		—	—	—	—	—	—	—	—	1
<i>Atheta</i> species indet.		—	—	—	—	—	—	—	—	121
Hydrophilidae										
<i>Megasternum boletophagum</i> Mrsh. .	8	11	—	1	—	—	—	—	—	20
<i>Helophorus granularis</i> L.	4	—	—	—	—	—	—	—	—	4
<i>Helophorus brevipalpis</i> Bedel = <i>griseus</i> Hrbst. . . .	2	2	1	—	—	1	—	—	—	6
<i>Cercyon pygmaeus</i> Illig.	1	3	—	—	—	—	—	—	—	4
<i>Cercyon tristis</i> Illig.	—	8	114	4	—	—	—	—	—	126
<i>Sphaeridium scarabaeoides</i> L. . . .	—	1	—	—	—	1	1	—	—	3
<i>Cercyon melanocephalus</i> L.	—	—	2	1	—	—	—	—	—	3
Scarabaeidae										
<i>Aegialia arenaria</i> F.	71	130	24	100	14	11	16	4	370	
<i>Anomala aenea</i> DeG. (ad.+l.) .	2	1	1	3	6	3	2	3	167	
<i>Aphodius fossor</i> L.	1	—	—	—	—	—	—	1	2	
<i>Aphodius fimetarius</i> L.	—	2	5	1	1	2	—	—	11	
Histeridae										
<i>Saprinus maritimus</i> Steph.	1	2	2	2	—	—	—	—	—	7
<i>Saprinus metallicus</i> Hrbst.	1	1	1	—	1	—	—	—	—	3
<i>S. rubripes v. arenarius</i> Marsh . .	—	2	1	—	—	—	—	—	—	3
<i>Saprinus rubripes</i> Er.	1	1	—	3	—	—	—	—	—	5
<i>Saprinus aeneus</i> F.	—	—	—	1	—	—	—	—	—	1

Family and species	S.P.A. no.	1	2	3	4	5	6	7	8	tot.
Curculionidae										
<i>Ceutorrhynchus assimilis</i> Payk. . . .		2	11	7	2	—	—	—	—	22
<i>Rhinoncus castor</i> F.		2	—	—	—	—	—	—	—	2
<i>Sitona flavescens</i> Mrsh.		—	6	3	—	—	—	—	—	9
<i>Apion vorax</i> Hrbst.		—	—	2	2	—	—	—	—	4
<i>Oxytoma pomonae</i> F.		—	—	2	—	—	—	—	—	2
<i>Apion frumentarium</i> Payk.		—	—	1	2	—	—	—	—	3
<i>Philopedon plagiatum</i> Schal. (ad.+l.)		—	—	—	+2	+1	+1	+3	—	8
<i>Apion nigritarse</i> Kirby		—	—	—	2	—	—	—	—	2
<i>Apion flavipes</i> Payk.		—	—	—	1	1	—	1	—	3
<i>Philopedon germinatum</i> Schal. (l.)		—	—	—	—	—	—	—	2	2
<i>Phytonomus arator</i> L.		—	—	—	—	—	—	—	1	1
Coccinellidae										
<i>Coccinella XI-punctata</i> L. (ad.+l.)		10 +90	5 +13	7	24	14	8	6	2	181
a. <i>longula</i> Weise		—	1	—	—	—	—	—	—	
a. <i>IX-punctata</i> L.		—	—	—	—	—	—	—	1	
<i>Coccinella VII-punctata</i> L. (ad.+l.)		17 +14	15	1	9	51	22	47	20	186
<i>Coccinella X-punctata</i> L.										
= <i>C. variabilis</i> Hrbst.										
a. <i>scribae</i> Weise		1	—	1	—	—	—	—	—	4
a. <i>X-pustulata</i> L.		—	1	1	—	—	—	—	—	
<i>Halizia XIV-punctata</i> L.		1	1	—	—	1	—	—	—	3
<i>Scymnus apetzi</i> Muls.		1	—	—	—	—	—	—	—	1
<i>Anatis ocellata</i> L.		—	—	—	—	—	1	—	—	1
<i>Chilocorus bipustulatus</i> L. (ad.+l.)		—	—	—	—	—	—	2	7	10
<i>Adonia variegata</i> Goeze.		—	—	—	—	—	—	2	—	2
Elateridae										
<i>Limonius aeruginosus</i> Oliv. (ad.+l.)		— +3	— +16	— +11	+33	+11	+2	—	2	80
<i>Brachylacon murinus</i> L.		—	1	1	—	1	—	1	—	4
<i>Cardiophorus</i> spec. (l.)		—	—	1	3	4	1	2	—	11
Cantharidae										
<i>Rhagonycha fulva</i> Scop.		3	21	13	6	1	2	—	4	50
<i>Psilotrix cyaneus</i> Oliv. (ad.+l.) .		2	7	—	+1	+2	+1	1	—	34
<i>Cantharis bicolor</i> Hrbst.		—	—	1	1	—	—	—	—	2
<i>Malachinus marginellus</i> Oliv. . . .		—	—	—	1	1	2	—	—	4
<i>Cantharis fulvicollis</i> F.		—	—	1	—	—	—	—	—	1
Tenebrionidae										
<i>Phaleria cadaverina</i> Latr. (l.) . .		1	—	—	—	—	—	—	—	1
<i>Phylan gibbus</i> F. (ad.+l.)		—	—	—	+7	+19	+34	+11	+8	398
<i>Melanimon tibiale</i> F. (ad.+l.) . .		—	—	—	—	—	68	90	51	212
<i>Crypticus quisquilius</i> L. (l.) . . .		—	—	—	—	+1	+2	—	1	1

Family and species	S.P.A. no.	1	2	3	4	5	6	7	8	tot.
<i>Fucellia maritima</i> Hall.	2	1	—	—	—	—	—	—	—	3
<i>Coenosia pumila</i> Fall.	1	—	—	—	—	—	—	—	—	1
<i>Coenosia tricolor</i> Zett.	—	1	1	—	1	—	—	—	1	4
Empididae										
<i>Coryneta pallidiventris</i> Mg.	8	—	—	—	—	—	—	—	—	8
<i>Hybos culiciformis</i> F.	—	1	5	1	—	—	—	—	1	8
<i>Tachista sabulosa</i> Mg.	—	1	—	—	—	—	—	—	—	1
<i>Hybos grossipes</i> L.	—	—	3	1	—	—	—	—	1	5
<i>Drapetis setigera</i> Lw.	—	—	—	7	—	—	—	—	—	7
<i>Coryneta bicolor</i> Mg.	—	—	—	—	—	2	1	—	—	3
Chloropidae										
<i>Meromyza pratorum</i> Mg.	2	2	3	4	16	3	2	1	33	
<i>Platycephala planifrons</i> F.	1	—	—	—	—	—	—	—	—	1
Sphaeroceridae										
<i>Sphaerocera curvipes</i> Latr.	2	—	2	1	—	—	—	—	—	5
<i>Borborus</i> (= <i>Cypselia</i>) <i>ater</i> Mg.	2	—	1	—	—	—	—	—	—	3
<i>Sphaerocera pusilla</i> Latr.	1	—	—	1	—	—	—	—	—	2
<i>Limosina</i> (= <i>Leptocera</i>) <i>vagans</i> Hall.	1	—	—	—	—	—	—	—	—	1
<i>Limosina lutosa</i> Stenh.	1	—	—	—	—	—	—	—	—	1
<i>Borborus</i> (= <i>Trichiaspis</i>) <i>equinus</i> Fall.	—	—	1	1	—	—	—	—	—	2
Dryomyzidae										
<i>Helcomyza ustulata</i> Curtis.	2	1	—	—	—	—	—	—	—	3
Asilidae										
<i>Philonicus albiceps</i> Mg.	1	—	—	—	1	—	—	—	—	2
Stratiomyidae										
<i>Chloromyia formosa</i> Scop.	1	—	—	—	—	—	—	—	—	1
<i>Nemotelus notatus</i> Zett.	—	—	—	—	1	1	—	—	—	2
<i>Hoplodontia viridula</i> F.	—	—	—	—	—	—	1	—	—	1
Bibionidae										
<i>Dilophus humeralis</i> Zett.	1	—	—	—	—	—	—	—	—	1
<i>Dilophus febrilis</i> L.	—	2	7	—	—	—	—	—	—	9
Rhagionidae										
<i>Chrysophilus auratus</i> F.	—	2	—	—	—	—	—	—	—	2
Syrphidae										
<i>Lasiopticus pyrastris</i> L.	—	1	1	1	—	—	—	—	—	3
<i>Epistrophe</i> (= <i>Syrphus</i>) <i>balteata</i> de G.	—	1	—	—	—	—	—	1	—	2
<i>Syrphus vitripennis</i> Mg.	—	1	—	—	—	—	—	—	—	1
Phryneidae										
<i>Phryne punctata</i> F.	—	—	2	—	—	—	—	—	—	2
Ephydriidae										
<i>Hydrina punctatonervosa</i> Fall.	—	—	—	—	—	12	2	—	—	14

Family and species	S.P.A. no.	1	2	3	4	5	6	7	8	tot.
<i>Hyadina guttata</i> Fall.	—	—	—	—	—	1	—	—	—	1
<i>Psilopa roderi</i> Girsch*)	—	—	—	—	—	—	1	—	2	3
Tabanidae										
<i>Chrysazona pluvialis</i> L.	—	—	—	—	—	1	—	—	—	1
<i>Therioplectus tropicus</i> Panz.	—	—	—	—	—	—	1	—	—	1
Dolichopodidae										
<i>Dolichopus agilis</i> Mg.	—	—	—	—	—	1	—	—	—	1
<i>Medetera micacea</i> Lw.	—	—	—	—	—	—	—	—	—	9
Lauxaniidae										
<i>Minettia desmometopa</i> de Mey.	—	—	—	—	—	—	—	2	2	4
Tryptidae										
<i>Noeeta pupillata</i> Fall.	—	—	—	—	—	—	—	1	—	1
<i>Rhagoletis batavae</i> Hering**)	—	—	—	—	—	—	—	—	1	1
Tipulidae										
<i>Tipula oleracea</i> L.	—	—	—	—	—	—	—	1	—	1
HOMOPTERA										
Jassidae										
<i>Psammotettix maritimus</i> Perr.	88	19	18	21	2	2	—	—	—	150
<i>Psammotettix sabulicola</i> Curt.	1	1	—	3	2	—	—	—	—	7
<i>Euscelis plebejus</i> Zett.	—	2	3	2	—	—	—	—	—	7
<i>Agallia venosa</i> Fall.	—	1	—	2	—	4	4	2	2	13
<i>Aphrodes bicinctus</i> Schrk.	—	—	—	1	13	16	13	12	55	55
<i>Mocydiopsis attenuata</i> Germ.	—	—	—	—	—	5	—	10	15	15
<i>Paropis scanica</i> Fall.	—	—	—	—	—	—	1	2	3	3
<i>Aphrodes histrionicus</i> F.	—	—	—	—	—	—	—	1	1	1
<i>Rhytidostylus proceps</i> Kbm.	—	—	—	—	—	—	—	—	1	1
Cercopidae										
<i>Neophilaenus pallidus</i> Hpt.	80	242	151	1150	1333	643	90	40	3729	3729
<i>Philaenus spumarius</i> L.	1	3	—	1	216	27	83	74	405	405
Delphacidae										
<i>Callipygona pellucida</i> F.	1	2	—	—	—	2	—	1	6	6
<i>Callipygona boldi</i> Scott.	—	—	—	—	—	1	1	—	2	2
Psyllidae										
<i>Psylla hippophaës</i> Frst.	—	—	—	—	—	—	470	27	497	497
NEUROPTERA										
Hemerobiidae										
<i>Micromus variegatus</i> F.	—	—	—	—	—	—	—	2	—	2
Chrysopidae										
<i>Chrysopa abbreviata</i> Curt.	—	—	—	—	—	—	1	1	1	3

*) Appeared to be a new species for the Dutch fauna.

**) Proved to be a new species.

Family and species	S.P.A. no.	1	2	3	4	5	6	7	8	tot.
HETEROPTERA										
Miridae										
<i>Trigonotylus psammaecolor</i> Reut. .	38	28	4	—	—	—	1	—	—	71
<i>Phytocoris varipes</i> Boh.	1	1	27	12	9	10	9	28	—	97
<i>Notostira erratica</i> L.	1	—	1	1	1	—	—	—	—	4
<i>Adelphocoris lineolatus</i> Goeze . .	—	—	—	—	—	—	—	—	1	1
Coreidae										
<i>Chorosoma schillingi</i> Schill.	—	4	—	4	21	22	13	9	—	73
<i>Rhopalus parumpunctatus</i> Schill. . .	—	—	—	—	17	17	15	11	—	60
Nabidae										
<i>Nabis major</i> Costa	—	1	—	—	4	3	5	11	—	24
<i>Nabis rugosus</i> L.	—	—	—	1	7	4	13	—	24	49
<i>Nabis fenus</i> L.	—	—	—	—	—	2	2	146	—	150
Neidae										
<i>Neides tipularius</i> L.	—	—	—	1	4	3	4	3	—	15
Lygaeidae										
<i>Gonianotus marginepunctatus</i> Wlff. .	—	—	—	2	8	8	48	19	—	85
<i>Cymus claviculus</i> Fall.	—	—	—	1	—	—	—	—	—	1
<i>Pionosomus varius</i> Wlff.	—	—	—	—	1	—	1	3	—	5
<i>Trapezonotus arenarius</i> L.	—	—	—	—	—	—	3	4	—	7
<i>Scolopostethus decoratus</i> Hhn. . .	—	—	—	—	—	—	—	1	—	1
<i>Stygnocoris pedestris</i> Fall.	—	—	—	—	—	—	—	12	—	12
<i>Nysius thymi</i> Wlff.	—	—	—	—	—	—	—	1	—	1
Pentatomidae										
<i>Dolycoris baccarum</i> L.	—	—	—	1	1	1	—	—	—	3
<i>Sciocoris cursitans</i> F.	—	—	—	—	—	—	8	23	—	31
<i>Odontoscelis dorsalis</i> F.	—	—	—	—	—	—	1	—	—	1
Saldidae										
<i>Saldula pallipes</i> F.	—	—	1	—	—	—	—	—	—	1
<i>Saldula saltatoria</i> L.	—	—	1	—	—	—	—	—	—	1
<i>Saldula orthochila</i> Fieb.	—	—	—	—	1	—	—	—	—	1
Reduviidae										
<i>Coranus subapterus</i> De G.	—	—	—	3	—	—	—	—	—	3
ORTHOPTERA										
Acrididae										
<i>Myrmeleotettix maculatus</i> Thunb. .	—	—	—	—	—	1	—	—	6	7
<i>Acridium subulatum</i> L.	—	—	1	—	—	—	—	—	—	1
<i>Platycleis albopunctatus</i> Fieb. . .	—	—	—	—	—	—	—	—	2	2
PSOCOPTERA (= COPEOGNATHA)										
Psocidae										
<i>Graphopsocus cruciatus</i> F.	—	22	9	33	49	35	59	55	262	

Family and species	S.P.A. no.	1	2	3	4	5	6	7	8	tot.
TRICHOPTERA										
Phryganeidae										
<i>Limnophilus affinis</i> Curt.	.	.	.	—	—	2	—	—	—	2
LEPIDOPTERA										
Noctuidae										
<i>Miana bicoloria</i> Vill.	.	.	.	—	—	2	—	—	—	2
<i>Caradrina IV-punctata</i> F.	.	.	.	—	—	1	—	—	—	1
<i>Caradrina taraxaci</i> Hb.	.	.	.	—	—	—	1	—	—	1
<i>Agrotis agathina</i> Dup.	.	.	.	—	—	—	—	—	1	1
<i>Leucania</i> spec.	.	.	.	—	—	1	—	—	—	1
Arctiidae										
<i>Coscinia cribrum</i> L.	.	.	.	—	—	—	—	1	—	1
Lymantriidae										
<i>Euproctis chrysorrhoea</i> L.	.	.	.	—	—	1	—	—	5	12
Geometridae										
<i>Abraxas grossulariata</i> L.	.	.	.	—	1	—	—	—	—	1
Gelechiidae										
<i>Bryotropha affinis</i> Dgl.	.	.	.	1	—	—	—	—	—	2
<i>Gelechia semicandrella</i> Stt.	.	.	.	—	1	—	—	—	—	1
<i>Bryotropha senectella</i> Z.	.	.	.	—	—	—	6	3	1	10
<i>Gelechia maculifera</i> Dgl.	.	.	.	—	—	—	2	1	—	5
<i>Gelechia marmorea</i> Hw.	.	.	.	—	—	—	1	4	5	16
<i>Bryotropha terrella</i> Hb.	.	.	.	—	—	—	1	—	—	1
spec. div. indet.	.	.	.	4	2	3	3	36	22	26
BLATTARIA										
Blattidae										
<i>Ectobius panzeri</i> Steph.	.	.	.	—	1	—	4	14	8	17
ARANEINA										
Micriphantidae (= Erigonidae)										
<i>Erigone arctica</i> White.	.	.	.	24	61	5	—	1	—	91
<i>Hypomma bituberculatum</i> Wider.	.	.	.	—	1	7	11	—	—	19
<i>Metopobactrus prominulus</i> Cbr.	.	.	.	—	1	—	9	7	1	22
<i>Entelecara erythropus</i> Wstr.	.	.	.	—	—	1	45	17	2	65
<i>Erigone atra</i> Blw.	.	.	.	—	—	—	1	—	—	1
<i>Stylocetor romanus</i> Cbr.	.	.	.	—	—	—	6	38	30	2
<i>Erigone atra</i> Blw.	.	.	.	—	—	—	1	—	—	1
<i>Oedothorax retusus</i> Wstr.	.	.	.	—	—	—	1	—	—	1
<i>Pocadicnemis pumila</i> Blw.	.	.	.	—	—	—	—	—	3	1
<i>Troxochrus scabriculus</i> Wstr.	.	.	.	—	—	—	—	—	1	4
<i>Cornicularia unicornis</i> Cbr.	.	.	.	—	—	—	—	—	1	2
Micriph. spec. div. juv. indet.	.	.	.	1	3	10	59	57	58	28

Family and species	S.P.A. no.	1	2	3	4	5	6	7	8	tot.
Thomisidae										
<i>Philodromus fallax</i> Snd.	13	31	6	5	—	—	1	—	56	
<i>Tibellus maritimus</i> Menge	—	—	—	2	4	—	—	—	—	6
<i>Oxyptila</i> spec. cf. <i>atomaria</i> Panz.	—	—	—	—	—	—	1	1	—	2
<i>Tibellus</i> spec. juv.	—	1	2	59	42	19	7	3	—	
<i>Xysticus</i> spec. juv.	—	3	—	1	3	2	5	7	—	
<i>Thanatus</i> spec. juv.	—	—	—	10	12	31	5	3	—	
Linyphiidae										
<i>Bathyphantes gracilis</i> Blw.	1	—	—	1	—	—	—	—	—	2
<i>Leptphyantes tenuis</i> Blw.	—	1	—	2	—	1	—	—	2	6
<i>Linyphia triangularis</i> Cl.	—	1	—	—	—	—	5	2	—	8
<i>Bolyphantes luteolus</i> Blw.	—	—	1	—	—	—	—	3	—	4
<i>Stemoniphantes lineatus</i> L.	—	—	—	23	4	9	5	7	—	48
<i>Floronia bucculenta</i> Cl.	—	—	—	—	—	—	—	2	—	2
<i>Linyphia peltata</i> Wider.	—	—	—	—	—	—	—	1	—	1
<i>Linyphiidae</i> spec. div. juv. indet.	1	—	—	4	34	4	13	35	—	
<i>Leptphyantes</i> spec. juv. indet.	—	—	—	—	—	—	—	5	—	
Lycosidae										
<i>Arctosa perita</i> Latr.	—	18	1	26	13	22	14	15	—	109
<i>Tarentula</i> (= <i>Alopecosa</i>) <i>fabrilis</i> Cl.	—	—	—	—	—	—	7	1	—	8
<i>Lycosa monticola</i> Cl.	—	—	—	—	—	—	1	—	—	1
<i>Lycosa</i> spec. div. juv. indet.	—	—	—	5	9	6	—	—	—	5
<i>Tarentula</i> spec. juv. indet.	—	—	—	—	—	—	1	—	—	
<i>Arctosa</i> spec. juv. indet.	—	—	—	—	—	—	—	5	—	
<i>Trochosa</i> spec. juv. indet.	—	—	—	—	—	—	—	—	2	
Clubionidae										
<i>Clubiona similis</i> L. Koch.	—	—	2	5	6	2	1	—	—	16
<i>Clubiona stagnatilis</i> Kulc.	—	—	—	—	1	—	—	—	—	1
<i>Clubiona vegata</i> Simon.*	—	—	—	—	—	—	2	2	—	4
<i>Agroeca proxima</i> Cbr.	—	—	—	—	—	—	—	7	—	7
<i>Scotina gracilipes</i> (Blw.)	—	—	—	—	—	—	—	3	—	3
<i>Clubiona</i> spec. div. juv. indet.	—	2	—	13	23	27	26	27	—	
<i>Cheiracanthium</i> spec. juv. indet.	—	—	—	—	3	—	5	1	—	
Tetragnathidae										
<i>Tetragnatha extensa</i> L.	—	—	1	—	—	1	—	—	—	2
<i>Pachygnatha clercki</i> Snd.	—	—	—	1	—	—	—	—	—	1
<i>Tetragnatha</i> spec. juv. indet.	—	—	—	2	—	—	3	—	—	
Araneidae										
<i>Araneus cornutus</i> Cl. juv.	—	—	1	—	—	—	—	—	—	1
<i>Araneus adianthus</i> Walck.	—	—	—	1	—	—	—	—	1	2
<i>Araneus redii</i> Scop.	—	—	—	—	—	—	—	13	3	16
<i>Araneus quadratus</i> Cl. juv.	—	—	—	—	—	—	—	—	1	1
Dictynidae										
<i>Argenna subnigra</i> Cbr.	—	—	—	1	2	—	—	—	1	4
<i>Dictyna latens</i> Fabr.	—	—	—	—	—	—	2	—	—	2
<i>Dictyna</i> spec. juv. indet.	—	—	—	—	—	—	—	—	—	1

*) Appeared to be a new species for the Dutch fauna.

Family and species	S.P.A. no.	1	2	3	4	5	6	7	8	tot.
Gnaphosidae										
<i>Zelotes serotinus</i> L. Koch.	.	—	—	—	—	—	1	11	—	12
<i>Drassodes dalmatinus</i> L. Koch.	.	—	—	—	—	—	—	—	2	2
<i>Zelotes electus</i> C. L. Koch.	.	—	—	—	—	—	—	—	1	1
<i>Zelotes</i> spec. juv. indet.	.	—	—	—	—	—	2	2	6	
<i>Drassodes</i> spec. div. juv. indet.	.	1	2	1	8	3	15	43	22	
Theridiidae										
<i>Theridium impressum</i> L. Koch.	.	—	—	—	—	—	—	3	3	6
<i>Theridium ovatum</i> Cl.	.	—	—	—	—	—	—	2	1	3
<i>Theridium bimaculatum</i> L.	.	—	—	—	—	—	—	2	1	3
<i>Theridium sisypium</i> Cl.	.	—	—	—	—	—	—	2	1	3
Pisauridae										
<i>Pisaura mirabilis</i> Cl. juv.	.	—	—	—	—	—	—	—	1	1
Salticidae										
<i>Synageles venator</i> Lucas	.	—	—	—	12	7	5	6	5	35
<i>Hyctia nivoyi</i> Lucas	.	—	—	—	—	6	7	11	1	25
<i>Attulus saltator</i> Simon	.	—	—	—	—	—	5	—	—	5
<i>Phlegra fasciata</i> Hhn.	.	—	—	—	—	—	—	8	2	10
<i>Marpissa muscosa</i> Cl.	.	—	—	—	—	—	—	1	—	1
<i>Euophrys frontalis</i> Walck.	.	—	—	—	—	—	—	—	1	1
<i>Salticidae</i> spec. div. juv. indet.	.	1	—	—	2	2	1	1	3	
OPILIONES										
Phalangiidae										
<i>Phalangium opilio</i> L.	.	3	17	11	45	54	14	10	38	192
<i>Oligolophus agrestis</i> Meade juv.	.	—	—	—	2	—	—	—	—	2
CHELONETHI (=PSEUDOSCORPIONES)										
Cheliferidae										
<i>Chelifer latreillei</i> Leach	.	1	—	—	74	244	60	85	50	514
DIPLOPODA (= PROGONEATA)										
Julidae										
<i>Cylindrojulus frisius</i> Verh.	.	2	4	1	34	26	17	15	12	111

II. BIOCENOLOGY

1. Introduction

Phytocenological research has indicated that, in the vegetation of a certain type of habitat, a number of plant communities or phytocenoses may be discerned, which are characterized by a particular combination of species. The investigation of the vegetation only, however, gives an incomplete image of the biocenosis, because the fauna has not been incorporated, for the biocenosis must comprise vegetation and fauna together.

Table Ia. Synopsis of classes, orders, families, species and individuals, collected in the yellow dune range of Terschelling

Classis	Ordo	Familia	Species	Specimens
1. INSECTA	1. Coleoptera	22	146	4566
	2. Diptera	16	41	162
	3. Hymenoptera*)	11	61	248
	4. Heteroptera	8	24	697
	5. Lepidoptera	5	16	63
	6. Homoptera	4	14	4891
	7. Neuroptera	2	2	5
	8. Orthoptera	1	3	10
	9. Copeognatha	1	1	262
	10. Blattaria	1	1	54
	11. Trichoptera	1	1	2
2. ARACHNOIDEA	1. Araneina	12	54	709
	2. Opiliones	1	2	194
	3. Chelonethi	1	1	514
3. DIPLOPODA	1. Chilognatha	1	1	111
3	15	72	368	12488

*) 1952 collection has not yet been identified.

To the student of biocenosis the question remains whether the animal population of a certain biotope really contains a combination of species which is typical for the biocenosis. The results of a number of previous investigations reveal that a certain relation between vegetation and fauna indeed exists (cf. BRO LARSEN, 1936; WILLIAMS, 1936; RABELER, 1937; QUISPTEL, 1941; PALMGREN, 1941; WESTHOFF, 1942; MÖRZER BRUIJNS, 1947; GISIN, 1949; KONTKANEN, 1950; MACFADYEN, 1952; BARNES, 1953).

A phytocenological inventory is made far more easily than a zoocenological one*). As a matter of fact, the former can be more sharply defined than the latter. Animals (especially birds and flying insects) are very mobile and in many cases are moving easily from one biotope to another. A considerable number of species are difficult to collect because of their mobility. Others are hiding in the vegetation, trying to escape the efforts of the investigator. Their number is considerably greater than that of the plants. Furthermore the identification of many animal species is difficult and invites a specialist's attention.

A quantitative inventory of quarter of a square metre of ground covered by dense vegetation takes about 3 hours concentrated work, followed by a tiresome identification. Considering these facts, it may be superfluous to mention that results of biocenological investigation have been rather scanty so far. During the last few years the following scientists have been occupied in this field of research:

*) MÖRZER BRUYNS (1947); GISIN (1949) and THÉODORIDÈS (1950) have pointed out, that the expression "zoosociology" should not be used in the same sense as phytosociology or plant sociology, as the former expression comprises the study of social groups, generally of only one species, such as are found in Hymenopteres and Isopteres. Botanists, too, are trying to eliminate the misleading expression of "sociology" by speaking of phytocenology.

AGRELL (1941, 1945): Collembola; QUISPTEL (1941): Formicidae; WESTHOFF & WESTHOFF- DE JONCHEERE (1942): Formicidae; RENKONEN (1944): Carabidae & Staphylinidae; MÖRZER BRUIJNS (1947): Gasteropoda; GISIN, (1947, 1949): Collembola; KONTKANEN (1948, 1949, 1950): Cicadariae; KRAMER & VAN HEERDT, (1950): Formicidae; MACFADYEN (1952): Microarthropoda; BARNES (1953): Araneina.

Phytocenological data of different authors may be compared successfully today, but in zoocenology development has not yet reached this level, as considerable differences in nomenclature, interpretation and methods of research are still found. Earlier efforts have been made to coordinate the results in both fields (GAMS, 1918; KLUGH, 1923) but only in the past 20 years have attempts to this end been successful.

The conception of "biocenosis" was first established by MOEBIUS (1877) and comprises all living individuals in a certain biotope, plants, as well as animals. Biocenosis has been very well defined by RESVOY (cit. THIENEMANN, 1925, p. 590): "A biocenosis is a well balanced system of living organisms, adapted to certain ecological circumstances". So the biocenosis is the unit of biocenology and represents the mean value of a number of observations, which have been carried out in a certain sampling unit (square or volume). For theoretical consideration we refer to: RENKONEN (1938); MÖRZER BRUYNS (1947, p. 47); GISIN (1947, 1949) and THÉODORIDÈS (1950).

It is a common practice in biocenological research to start from the phytocenological units, the associations, with their corresponding plant communities. However, to make a pure survey of the relations of the fauna and the abiotic environment, it is advisable to investigate the distribution of the animals in the habitat detached from the plant communities, because this is the only way to probe the relations between the communities. In some cases they will overlap each other, in others there will be differences in the limits of cenoses. The results of various authors are strongly diverging in this point of view (viz. GISIN, 1947, p. 63). Undoubtedly it is premature to draw definite conclusions in this field of research: inefficient sampling technique, disparity of sampling methods, faulty interpretations and insufficient data for statistical analysis are causing these difficulties (cf. the contradiction AGRELL-GISIN : GISIN, 1947, p. 63).

The investigation of the biocenoses in their full extent is a hardly practicable assignment, and so many scientists have turned to means of accomplishing at least part of the whole job: H. KROGERUS (1948). Others confined themselves to investigating one systematic unit in certain habitats, e.g., AGRELL (l.c.) and GISIN (l.c.) who studied the Collembola in a number of biotopes in Sweden, and in Switzerland, respectively. MÖRZER BRUYNS (l.c.) investigated the relations between the vegetation and the Gastropoda at Gorssel (prov. Gelderland, the Netherlands) and KONTKANEN (l.c.) worked on the zoocenoses of Cicadariae (Homoptera) in Finland. BARNES (l.c.) studied the spiders of maritime communities at Beaufort N.C., U.S.A. VAN DER DRIFT (l.c.) approached the problem in another way, by obtaining the biggest possible part of the biocenosis of one biotope (beech-wood near Hoenderloo, prov. Gelderland, the Netherlands) in a thorough investigation.

It is our object to present the results of a study of correlations between the

vegetation and the entire macrofauna (for the definition of this conception cf. VAN DER DRIFT 1950, p. 25) — as far as possible — of the duneland habitat. The field research has been completed by autecological data derived from references.

2. The yellow dune region

The duneland habitat that has been investigated is a part of the Nature Reserve 'Boschplaat' on the island of Terschelling, one of the Westfrisian isles in the most Northern part of the Netherlands (fig. 1). It occupies the yellow dune-range

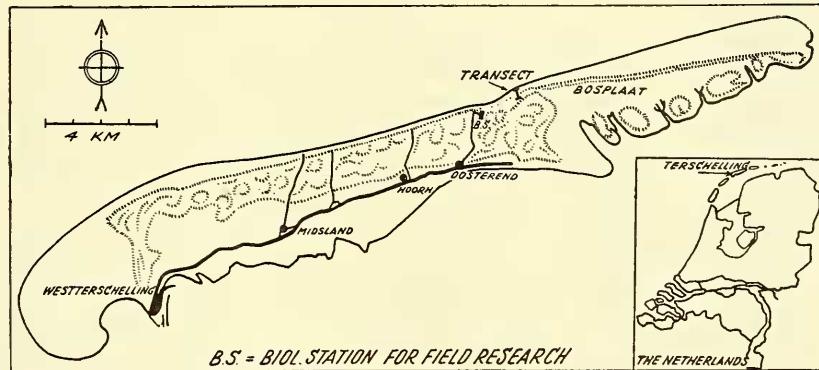


Fig. 1. Map of the Isle of Terschelling.

between km mark 19 and 20 (fig. 2. Dune profile). These yellow dunes originated by the action of three factors: sand, wind, and the activity of certain plant species (cf. VAN DIEREN, 1934; WESTHOFF, 1947).

(a) Climate.

In general the climate is strongly influenced by the sea. Extreme temperatures seldom occur. The winter is milder and shorter, the summer cooler and longer than in the central and more continental parts of the country. The proximity of the North Sea causes the temperature to change more slowly than on the continent. The days with frost are far less than inland — 42.2 days as compared to 74.4 days — and the period over which they are distributed is much shorter. The hottest month is August instead of July. On the contrary, the micro-climate also in the yellow dunes is liable to strong fluctuations. The arid conditions are accentuated by the high daytime temperatures that can be attained on sunny days. On August 7th, 1950, a temperature of 45° C has been registered at 12.30 p.m. in a denuded patch on the S-slope of a small dune, and in a sheltered spot even 52° C was found. At the same time, temperature on the N-slope only amounted to 24° C. Under passing clouds, shorttime fluctuations of temperature, especially near the surface, are very marked: a drop of 10—15° C frequently occurs.

Graph 1 shows a general survey of the course of temperature and humidity in an *Ammophila*-tussock during 30 hours. Though the data were not taken during

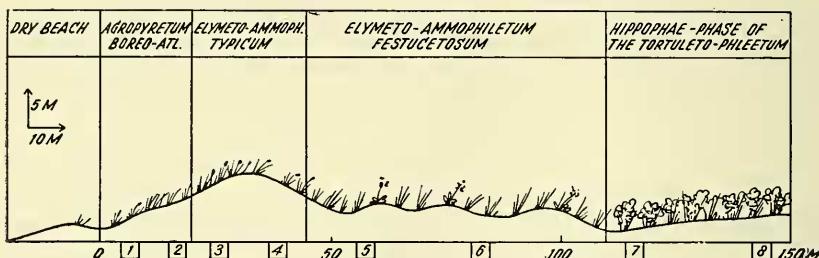


Fig. 2. Transect through the yellow dune region of Terschelling.

the 1950—1952 period, but in 1955 in a similar biotope, they give a good picture of the microclimatic relations in a tuft of Marram grass.

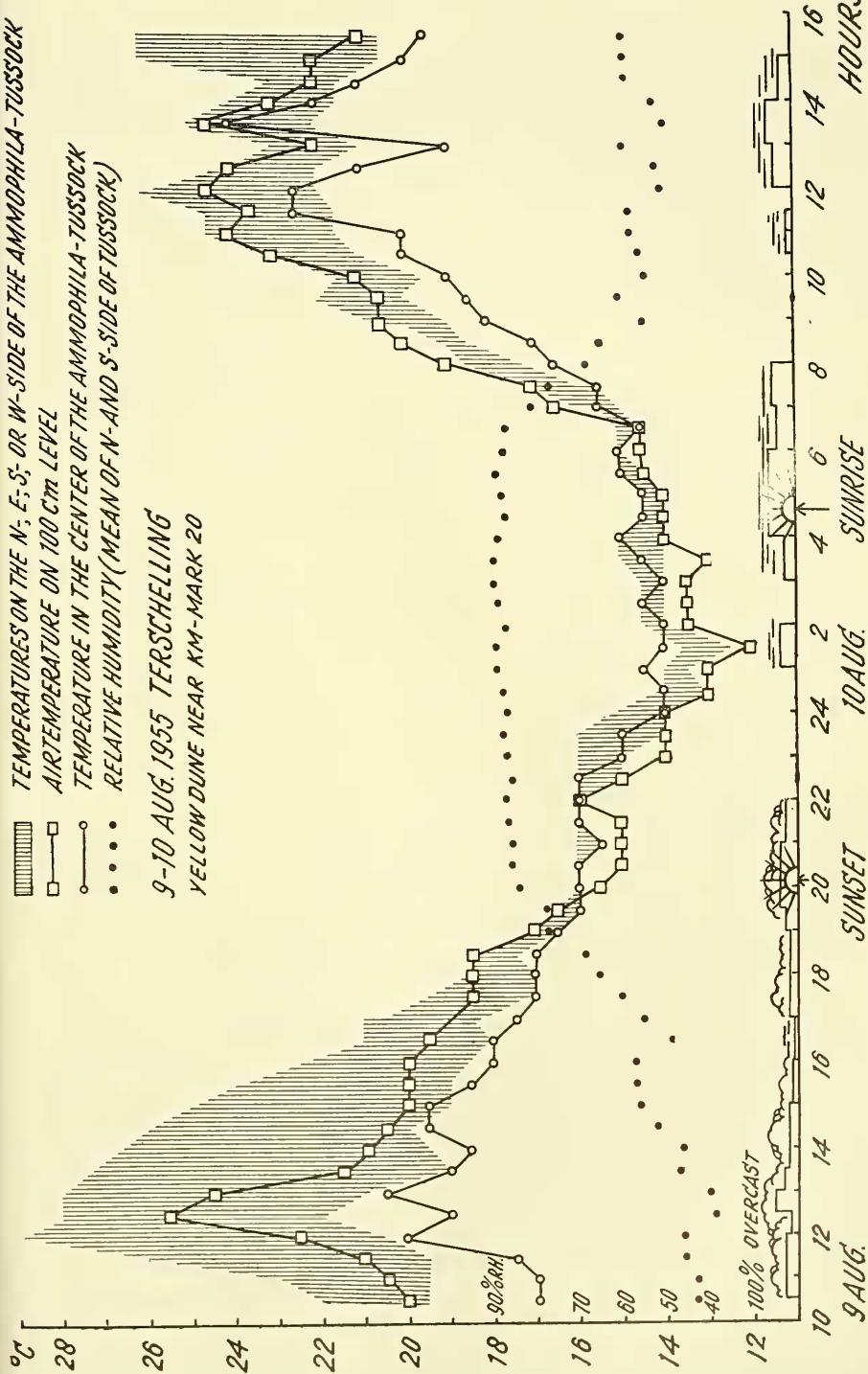
It is especially interesting to note that temperature in the centre of the tussock during daytime is always lower than air temperature at 1 m, but after sunset this phenomenon is reversed and the air temperature drops below the temperature in the centre of the tuft; which clearly proves its sheltering function.

According to VAN DIEREN (1934), in the calm cloudless night of August 3rd, 1932, the minimum temperature of 2.8° C was registered. On the other hand, at a depth of 10 cm in the sand temperature oscillates between 20—22° C on both the N-slope and the S-slope. These fluctuations certainly affect the selection of plants and animals. On the N-slope the sand becomes damp a few inches below the surface, whereas on the S-slope it is strongly desiccated by the heat of the sun during cloudless days. The desiccation prevents absorption of moisture in rainy periods, the water running along the surface. The influence on the vegetation is obvious: only few plant species will germinate in this environment and only few seedlings will be able to survive such severe conditions (VAN DIEREN, 1932; SALISBURY, 1952).

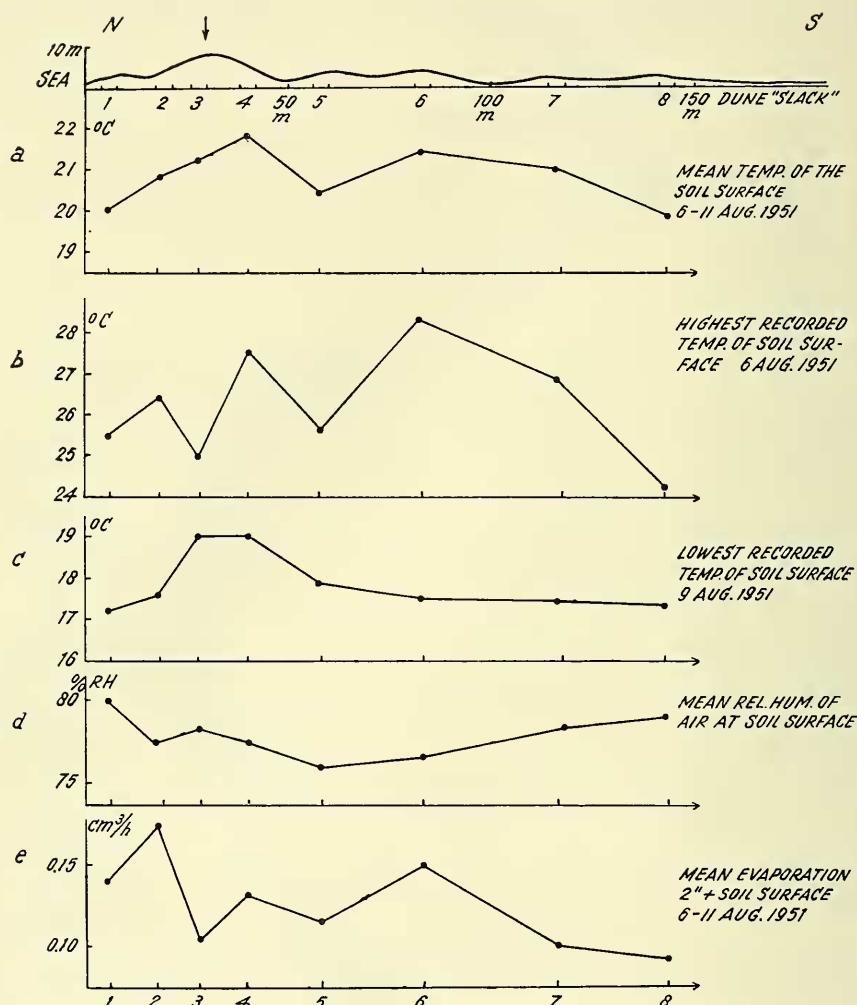
During the 1951 survey, microclimatic data have been collected during those days, when an inventory was made in the sampling area (6-7-9-10-11 Aug.). They represent the mean values of the records taken at 10-11-12-13-15-16-17 hrs. In graph 2 temperature and humidity of the soil surface are plotted against the sampling squares in the transect.

The mean soil surface temperature (graph 2a) which is fairly low in the small fore-dunes, gradually rises and attains its highest value on the landward face of the main dune range (sample plot no. 4) which has a very sheltered position. A marked drop is shown in sample plot no. 5, which is situated on the north slope of the lower inland dune. Sample plot no. 6 again, has a higher surface temperature, caused by its situation on the S. slope of this lower dune. In sample plots nos. 7 and 8 temperature values tend to be lower, as a consequence of shadow, cast by dense vegetation (*Hippophaë* !) in these sites.

Graph 2b shows the highest mean temperature recorded during a sample day (August 6th, 1951). It gives about the same picture as the general mean (graph 2a), but the temperature in sample plot no. 3 shows a sudden drop, which is probably caused by the strong onshore (N.) wind on that day, this sample plot being the most elevated and exposed site on the windward face, of the main dune ridge. Also surface temperature in sample plot no. 6 is higher than in no. 4,



Graph 1. General survey of the course of temperature and humidity in an *Ammophila* tuft during 30 hours.



Graph 2. Microclimatic observations in the yellow dune region of Terschelling.

probably due to its situation on the S. slope and more inland than the former.

Graph 2c gives a picture of temperature records on a day with a heavy, low overcast (Aug. 9th, 1951) and a S.W. off-shore wind. The situation is more or less reversed, the highest temperatures being registered in the sheltered sample plot no. 4, and in no. 3 which is now situated on the leeward side of the ridge. The same goes for sample plots no. 6 and no. 5, where the former is now on the windward of the lower inland dune and the latter on the leeward face.

The relative humidity was recorded by means of a small aspiration hygrometer, which could be placed easily between dense vegetation. The results however, are not very spectacular, as the mean value oscillates between 75 and 80 percent. In general, when temperature drops, rel. hum. rises. In sample plot no. 1, nearest to the sea, and in the dense vegetation of sample plots no. 7 and 8, R.H. reaches

its maximum value. It is the authors' impression that the R.H. does not play an important part in the distribution of insects in the yellow dune range (Graph 2d).

Apart from the R.H., data of evaporation were also taken in the transect. Eight simple evaporimeters, kindly supplied by Dr. R. J. v. d. LINDEN (I.T.B.O.N., Arnhem) were placed near the sampling squares. Peaks of evaporation are found at sample plots no. 2 (influence of onshore wind), no. 4 and 6 (high temperature on S-slope).

In sample plots no. 7 and 8 dense vegetation provides an efficient sheltering effect and evaporation shows a marked drop. The same goes to some extent for sample plot no. 5, where its position on the N-slope, directly behind the main ridge provides a sheltered site (graph 2e).

(b). Soil characters.

The dunes of the Westfrisian Isles contain a relatively small amount of calcium carbonates, unlike the dunes south of Bergen (prov. N. Holland). This fact may be ascribed to the small number of shells which are washed ashore in this region. According to WESTHOFF (1947) this phenomenon is of great influence on the vegetation as can be seen, for example, in the poor growth of the Sea Buckthorn (*Hippophaë rhamnoides*). The poverty in calcium carbonate of the dunes becomes especially evident in the inland part of the investigated area.

The property of the soil in the yellow dune range is at the outset an important factor from a biological point of view. Its extreme mobility is the feature which is most significant in relation to animal and plant life. The grains of wind-borne sand are carried inland from the sandy expanses exposed at low water, which is dried by the agency of sun and wind. In the yellow dunes this mobility is sometimes manifest in removal by wind, at others in rapid addition (pl. 24), which inhibits the survival of any but highly specialised organisms (e.g. *Agropyron junceum*). Moreover the youngest lowest stages of the yellow dunes are liable to inundation, and inevitably are subject to windblown spray. The organisms living there, must consequently be able to withstand the vagaries of a shifting and arid medium and occasionally inundation by sea water. Since the agent of transport is air movement, the decline of velocity of wind action brings about the shedding of nearly all airborne particles behind the main yellow dune ridge.

The calcium, nitrate and phosphate content of the yellow dunes which may already be low at the outset, will become still lower inland as leaching proceeds, and in accordance with these facts, the pH declines correspondingly (WESTHOFF, 1947). Only a small amount of organic matter is met with in this area, and the buried vegetation leaves only faint layers of humus in the sand. The salt-content is originally high in the low hummocky fore dunes, which are occasionally covered by seawater during very high tides, but drops sharply more inland.

(c). Vegetation.

The high tide puts down on the beach at the drift line a certain amount of organic matter (seaweed, dead animals), which supply nutrients*) and especially

*) Analysis of the soil of one such drift line showed a high content of calcium (4–9%) and potash (2.04% K₂O) and an appreciable amount of phosphorus (0.39% P₂O₅). The chloride content was low, — viz., 0.16%, doubtless due to leaching by rain (SALISBURY, 1952, p. 207).

nitrates for annuals, such as Sea Rocket (*Cakile maritima*) and Prickly Saltwort (*Salsola Kali*). Also must be mentioned the Sea Wheat Grass (*Agropyron junceum*), a perennial grass which is extremely tolerant of sea water and plays an important part in the formation of embryo dunes. The grass has a rather low top-growth and is not a very efficient collector of sand as its extension is more horizontal than vertical, so by itself, the Sea Wheat Grass only forms small fore dunes. The plants may become completely buried during the winter months and the next year the grass grows through to the new surface, often branching in the process. Burial commonly involves development of lateral buds so the young dune is penetrated by a network of rhizomes and shoots.

When the embryo dune is about 1 m high, another perennial grass, and by far the most important pioneer dune plant on the West-European coasts, the Marram Grass (*Ammophila arenaria*) becomes the main dune builder in collaboration with the Lyme Grass (*Elymus arenarius*), which, however, plays a minor part in this function. Compared with the Wheat Grass, the Marram Grass has a stiffer, more erect habit and the tufts of its long leaves may project from 60 to 90 cm above the dune surface. It is very efficient in diminishing the force of the wind and brings about the deposition of more sand. The *Agropyron*, *Ammophila* and *Elymus* may only develop successfully if wind-borne sand, containing nutrients (carbonate, nitrate and phosphate) from the drift line, is continuously supplied. Where transport subsides and the sand is shed behind the first ridge of dunes, *Ammophila* and *Elymus* are less viable. Red festuce (*Festuca rubra* var. *dumetorum*), Evening Primrose (*Oenothera biennis* var. *arenaria*), Creeping Sow-Thistle (*Sonchus arvensis*) make their appearance, followed by the Sea Buckthorn (*Hippophaë rhamnooides*). In the leached out dunes more inland, Sheep's-bit (*Jasione montana*), Hair Grass (*Corynephorus canescens*), Mouse-ear Chickweed (*Ceratium semidecandrum*) are abundant. In dry sandy patches and under the *Hippophaë*-scrubs one may meet the Mosses *Brachythecium albicans*, *Hypnum cupressiforme*, and *Tortula ruralis*. (VAN DIEREN, 1934, WESTHOFF, 1947, SALISBURY, 1952). The plant communities which are of major interest in this region, will be more fully described in this paper.

(d). General condition of life in the area of study.

The conditions in the duneland habitat are very complicated and it is impossible to present a complete recapitulation here. In the meantime research of insect ecology has revealed numerous data on the factors influencing insect life in relation to the qualities of the environment.

It will be evident that the water relations of the dune soils will play an important part as to the animal and plant life. The dryness of the dunes is almost wholly caused by their low capacity for water retention and the whole environment is favourable for rapid evaporation. Thus, especially on S. slopes, small temperate deserts come into being, which are not conditioned by climatic circumstances as in true deserts but by lack of capacity of the dune to retain water. Data from a number of dune systems obtained, both in spring and in summer, in periods of rain and during or after spells of drought, enable us to form a fairly clear picture of the water supply available to the living organisms in the dune area throughout the year

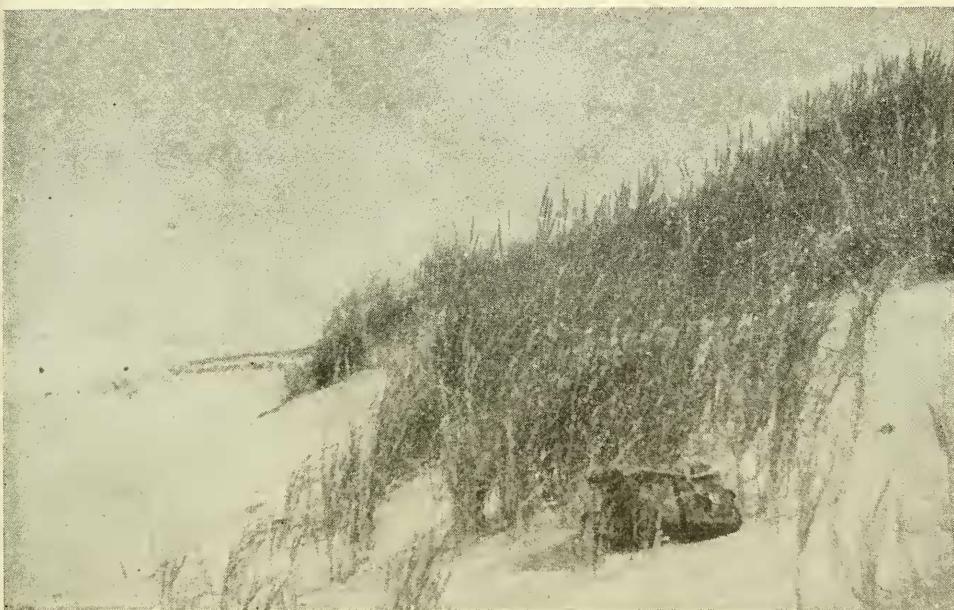


Fig. 3. *Agropyretum boreo-atlanticum*, sample plot no. 1 (Eastward view).



Fig. 4. *Elymeto-ammophiletum typicum*, seaward face of the main dune ridge, sample plot no. 3 (Westward view).



Fig. 5. *Elymeto-ammophiletum typicum*, landward face of the main dune ridge, sample plot no. 4 (Westward view).



Fig. 6. *Elymeto-ammophiletum festucetosum*, sample plots nos. 5 and 6. Illustration of the sampling method (Eastward view).

(SALISBURY, 1952, p. 171 seq.). The high daytime temperatures that can be attained on sunny days accentuate the arid conditions on the yellow dune system. However, though the surface temperatures may reach to over 50° C, no appreciable proportion of heat is transferred to the deeper layers, which remain cool and damp. In older dunes, organic matter increases the heat conduction of the soil, so that in sunshine the contrast between the surface temperature and that of the sand a little lower, is less marked (SALISBURY, 1952, p. 192).

The importance of the retention of heat near the surface is obvious, for the vegetation as well as for animal life. The roots of the dune plants are embedded in cool, wet sand, even on the hottest day, whereas fauna elements, by digging tunnels in the deeper layers, may protect themselves from desiccation.

Dense tufts of Marram Grass (*Ammophila arenaria*) may have a shading effect lowering the temperature by about 6° C, but under mosses and lichens in bright sunshine the surface temperatures are often appreciably higher than in bare areas, as a result of absorption of radiant energy by the dark colour of these plants and the absence of air currents (SALISBURY, 1952, p. 194, MÖRZER BRUYNS, in litt.).

From these facts it will be obvious that the conditions for the underground parts of perennials and for certain digging animals (e.g., Diplopoda, Coleoptera) are comparatively uniform, whereas dune annuals with shallow root systems and jumping, flying or climbing animals (Homoptera, Heteroptera, Diptera, Araneina) must endure marked fluctuations. This emphasizes the specialised nature of the environment and tends to reduce the number of species.

3. Phytocenological data

The phytocenological surveys of the four investigated zones were taken according to the methods of the Franco-Swiss school, as they allow for making a difference between units, which are ecologically comparable (cf. BRAUN BLANQUET, 1928).

The first number after the name of the species stands for quantitative estimation:

- 5 75—100% vegetable cover
- 4 50—75% vegetable cover
- 3 25—50% vegetable cover
- 2 5—25% vegetable cover or abundant but diffused
- 1 sparsely occurring
- + only a few individuals occurring.

The second number stands for sociability:

- 5 covering the total surface
- 4 in very big clusters
- 3 in big clusters
- 2 in small clusters
- 1 only dispersed individuals



Fig. 7. *Hippophaë*-phase of the *Tortuleto-phleetum*, sample plot no. 7 (Northward view).



Fig. 8. *Hippophaë*-phase of the *Tortuleto-phleetum*, sample plots nos. 7 and 8. (Southward view).

Sample plot no. 1 was situated on a small, well developed fore dune, covered with *Agropyron junceum*, no. 2 in the transition zone of the *Agropyretum boreo-atlanticum* to the *Elymeto-Ammophiletum typicum* (table II) which becomes evident in the development of the Marram Grass (fig. 3).

Table II. *Agropyretum boreo-atlanticum*

Sample plot number	1	2
Surface area	100 m ²	64 m ²
Cover of vegetation	40—50%	30—40%
Height of vegetation	30—40 cm	40—60 cm
<i>Agropyron junceum</i>	2/3.3	2.2
<i>Ammophila arenaria</i>	1.3	2.3
<i>Elymus arenarius</i>	+3	+2

Sample plot no. 3 was chosen in a site on the seaward face of the main dune ridge where the *Ammophiletum typicum* had a maximum development, caused by the constant supply of windborne sand (Table III). The tufts of Marram Grass showed an abundant growth and were flowering profusely. Their base was constantly buried by the shifting sand, as the dense clusters were very efficient catchers of the flying grains (fig. 4). Therefore, organic matter in the soil increases and development of fungi (*Inocybe* spec.) becomes possible.

Sample plot no. 4 was situated on the landward face of the main ridge, half-way of the slope. The supply of wind-borne sand had subsided, the Marram Grass was not so strongly developed and in other sites a subassociation of the *Ammophiletum* could be found, which contained Red Festuce and Sow-Thistle. (Table III). Sample plot no. 4, however, still was a good example of the typical Marram Grass vegetation in the yellow dune region. As will be shown afterwards, the development of the fauna in this area tends already to a relation with the *Ammophiletum festucetosum* (fig. 5).

Table III. *Elymeto-Ammophiletum typicum*

Sample plot number	3	4
Surface area	64 m ²	64 m ²
Cover of vegetation	30—40%	40%
Height of vegetation	50—60 cm	50—60 cm
<i>Ammophila arenaria</i>	3.3	3.3
<i>Elymus arenarius</i>	+2	1.3
<i>Agropyron junceum</i>	+2	1.2

In sample plot no. 5 the supply of wind-borne sand has subsided altogether and a number of plants which were absent thus far, are able to develop in the quieter atmosphere. Therefore, the vegetable cover becomes more dense (e.g. sample plot no. 6). Sea Wheat and Lyme Grass are diminishing in number and vitality, the latter suffers infection of an Ustilagine fungus, which could not be identified.

The Marram too shows less vitality: instead of luxuriant flowering tussocks we find still dense but usually sterile tufts with many dead shoots (table IV).

The occurrence of Cat's-Tail Grass (*Phleum arenarium*) points to a relationship with the *Tortuleto-Phleetum* community, which is typical for calm, hot, sandy regions containing calcium carbonate. This community will be found in the environments of the transect locally on S-slopes.

The same goes for sample plot no. 6 but in addition Sheep's-bit (*Jasione montana*) and Hair Grass (*Corynephorus canescens*), both characteristic for *Corynephoriion* may be found (table IV). These species are characteristic for leached-out soils with a low Ca-content, which cover wide expanses of the grey dune region. Sample plots nos. 5 and 6 are thus a fine demonstration of the gradual loss of Ca-carbonate of the inland dunes (fig. 6).

Table IV. Elymeto-Ammophiletum festucetosum

Sample plot number	5	6
Surface area	64 m ²	64 m ²
Cover of vegetation	40%	50—60%
Height of vegetation	50—60 cm	50—60 cm
<i>Ammophila arenaria</i>	3.3	4.3
<i>Elymus arenarius</i>	1.2	+.1
<i>Agropyron junceum</i> (veg.)	1.2	+.1
<i>Festuca rubra</i> var. <i>dumetorum</i>	1.2	+.2
<i>Oenothera biennis</i>	+.1/2	+.1
<i>Hieracium umbellatum</i>	1.1	2.2
<i>Sonchus arvensis</i>	+.1	+.1
<i>Cerastium semidecandrum</i> var. <i>tetrandrum</i> †	+.1	+.1
<i>Leontodon nudicaulis</i>	1.1	1.2
<i>Pbleum arenarium</i> †	+.1	1.2.
<i>Corynephorus canescens</i>		+.3
<i>Jasione montana</i>		+.1

The last zone investigated is the *Hippophaë*-phase of the *Tortuleto-Phleum* (table V), which occurs on the landward side of the *Ammophiletum festucetosum*. The Sea Buckthorn vegetation is comparatively thin and nowhere the shrubs get higher than 50—60 cm (figs. 7 and 8), whereas in the calcareous dunes on the mainland S of Schoorl it may reach a height of appr. 2 m.

According to WESTHOFF (1947, p. 92), this *Hippophaë*-phase as described for Terschelling is characteristic for the dune regions of the West-Frisian Isles, which are poor in lime; this phase has only a local distribution.

Comparing sample plots nos. 5 and 6 with 7 and 8, we see a good agreement in the local vegetations. The same species of the *E.-Ammophiletum festucetosum* are met with in the sample plots nos. 7 and 8 and moreover a few of the *Tortuleto-Phleetum*, e.g. *Phleum arenarium* and the Moss *Brachythecium albicans*. As might be expected, as one goes more inland, the species of the *Corynephorion* are increased in numbers and vitality.

Table V. *Hippophaë*-phase of the transition from the E.-Ammophiletum to the Tortuleto-Phleetum

Sample plot number		7	8
Surface area		64 m ²	40 m ²
Cover of vegetation		50—60%	75%
Height of vegetation		till 60 cm	till 70 cm
<i>Hippophaë rhamnoides</i>		2/3.2	4.3
<i>Ammophila arenaria</i>		3.3	2.3
<i>Hieracium umbellatum</i>		2.2	1.2
<i>Oenothera biennis</i>		2.2	2.1
<i>Brachythecium albicans</i>		1.3	1.3
<i>Corynephorus canescens</i>		+ .3	2.3
<i>Festuca rubra</i> var. <i>dumetorum</i>		+ .2	2.2
<i>Elymus arenarius</i> (veg.)		+ .1	+ .1
<i>Viola tricolor</i>		+ .1	
<i>Jasione montana</i>		+ .1	+ .1
<i>Leontodon nudicaulis</i>		+ .1	+ .1
<i>Phleum arenarium</i> †		+ .1	+ .1
<i>Cerastium semidecandrum</i> var. <i>tetrandrum</i> †		+ .1	+ .1

4. Zoocenological data

(a). Review of current methods

The most important object of biocenological research is the quantitative inventory of the sampling area, by which we are able to get an impression of the abundance of the animals collected in the different life-communities.

In order to establish the character of the zoocenoses in the four successive biotopes, which were characterised by the above mentioned phytocenoses (cf. p. 247 ssq.), the number of individuals collected in each square (16 m²) were counted. This number is called abundance.

It has been proved to be useful to express the number of individuals of a species in percents of the total numbers of animals, collected in the biotope that has been investigated. As a matter of fact it has been the custom to classify the species in "classes of dominance". KROGERUS (1932) speaks of "dominant", "influent" and "recedent" species, defined as representing respectively > 5 percent, 5—2 percent or < 2 percent of the total number of individuals.

It will be evident that dominant species will be most important in the structure of a biotope. SHELFORD & TOWLER (1925) even went so far as to nominate their zoocenoses after the dominant species. We think this procedure still premature in the light of present day development.

By means of the data, provided by arthropod synecology, different types of communities (Bestandes-type, RENKONEN 1938, p. 111) may be distinguished. According to RENKONEN (1938, p. 6, 16, 126) and some American synecologists, the animal communities can be classified on the basis of the fauna alone. To compare the communities of the dune area with RENKONEN's dominance affinity method proved to be unsuitable in our case.

We, therefore, adopted SØRENSEN's (1948) quotient of similarity (QS) method, based on faunal similarity. The principle of this method is the following.

If a sample A contains a species and sample B again b , and c of the species are common to both samples, the quotient of similarity (QS) is obtained from the formula

$$\frac{2c}{a + b} \times 100 = QS.$$

So the similarity of the samples is expressed as a percentage, and the result can be presented in the form of a trellis diagram.

The trellis diagram, also called square net diagram has first been used by KULCZYNSKI (1928), who arranged the percentages of mutual relationships of plant communities in a square. Along the upper side of the square the communities were written from left to right, and on the right side the same communities in the same sequence from top to base. The square is then divided into "columns" by which a network of small squares comes into being.

The mutual relationships of the communities are split up in groups of 10 percent (0, 10, 20%) and are represented in the diagram by different shading, the darkest shade standing for the highest percentage of relationship. So groups of communities with the darkest shade belong to the same type. This method has many advantages, as it is absolutely objective, though the comparison of great numbers of communities proves to be an utterly tiresome process. The natural relationships of the communities too, are very clearly demonstrated by the trellis diagram. In the dominance affinity method, the incidental high quantity of any given species without intrinsic value may exert too strong an influence on the index of affinity (RENKONEN 1938, p. 119). On the other hand, in the faunal QS method, species not actually belonging to the community which have spread from the surrounding areas, even though they may number no more than one individual each, may affect the QS value as much as the typical species of the biotope (cf. RENKONEN, 1938, p. 112). For this reason, species that apparently have strayed from strange surroundings into the sampling area, must be eliminated in QS determination.

Often, the results from both these methods will prove to be very different. In spite of the objectiveness of the quotient values, the concept of the community type in itself is always more or less subjective.

Still another method proves to be valuable for estimating the results of quantitative sampling. BARNES (1953) has expressed his results in terms of frequency and density, which allows a good comparison of the populations of different communities. Frequency, as used in his study (BARNES, l.c., p. 320), is a statistical expression of the number of times a particular species occurs in a given number of samples, all of which have been taken in the same concrete community. Density, on the other hand, is defined as the average number of individuals of a species per sample. BARNES (l.c.) believes that this use of the term "density" results in a more accurate expression of the insect population than its frequent use as the percentage of the total number of that species relative to the total number of specimens collected in all samples taken. This seems particularly to be true in a population of low density. In his frequency-density diagram, the ecological value of a species has been expressed as a product, which enables an easy way of comparison.

(b). Sampling methods.

A transect was drawn perpendicular to the coastline. It reaches across the main coastal dune ridge as far as the first "slack" behind the yellow dune area, in a site which was estimated to be representative for the yellow dune region of Terschelling.

The transect starts on the landward side of the beach at the base of the small embryo dunes, near the winter tidal mark and cuts through the following plant communities, characterized according to the Franco-Swiss vegetation-systematics:

The *Agropyretum boreo-atlanticum* (Sea Wheat Grass dunes);

The *Elymeto-Ammophiletum typicum* (Marram Grass community);

The *Elymeto-Ammophiletum festucetosum* (Degenerate phase of the Marram Grass community);

The *Hippophaë phase* (Sea Buckthorn phase) of the transition from the *Elymeto-Ammophiletum festucetosum* to the *Tortuleto-Phleetum* (*Tortula* Moss-Cat's Tail Grass community).

The transect had a length of 150 m and a width of 16 m. In each of the 8 sample plots the authors made a phytocenological analysis in that part of the transect, with a length of 4 m and a width of 16 m, before collecting started. The sample plot was divided into 4 squares of 4×4 m, which are situated side by side, parallel to the coastline. Each square was searched by two collaborators (mostly students in biology of Utrecht University), for fauna elements. In order to make the inventory qualitative and quantitative as well, the soil was stirred to a depth of 5 cm, every plant of the vegetation carefully scrutinized and finally removed. The animals that could be distinguished with the naked eye were collected by means of an aspirator and killed with ethylacetate afterwards. No mechanical means for collecting (e.g. sieves or nets) were used. In a few cases, when too small a number of collectors was available, only 2 or 3 squares were searched, especially in sample plot nr. 8, the last survey in the *Hippophaë* phase, where collecting was hampered by dense vegetation. The data, however, have been adapted to the mean sample plot area. To make an inventory of a 4×4 m in the yellow dune range takes 4—5 hours, dependent on the density of the vegetation.

It must be appreciated that the reliability of this sampling method depends for a major part on the skill and conscientiousness of the collector, so the results of this quantitative investigation will only approximate to the true relations. These facts, however, are not estimated to be a serious drawback as mechanical sampling methods also have their particular deficiencies, in which individuals are lost during extraction.

Sampling area no.	1, length,	4— 8 m;	area,	4×16 m ²	<i>Agropyretum boreo-atlant.</i>
"	2, "	17— 21 m;	"	4×16 m ²	"
"	3, "	26— 30 m;	"	4×16 m ²	<i>E.-Ammophiletum typicum</i>
"	4, "	38— 42 m;	"	4×16 m ²	"
"	5, "	56— 60 m;	"	4×16 m ²	<i>E. Ammophiletum festucetum</i>
"	6, "	81— 85 m;	"	4×16 m ²	"
"	7, "	114—118 m;	"	4×16 m ²	<i>Hippophaë phase</i>
"	8, "	133—137 m;	"	$2 \text{ à } 3 \times 16$ m ²	"

The nos. of the phytocenological sample plots correspond with the sample nos. of the zoological inventarisation.

For the total number of arthropods (orders, families, genera and species) collected, we refer to table I (page 227).

By a preliminary sampling expedition in 1947 in this area we could achieve an approximate idea of the species which are found in this region. This proved to be a great help in the identification in the years 1950—1951—1952 when definitive data were collected. The common species could easily be identified, the rare ones were sent to specialists which had been contacted previously in 1947.

We are especially grateful to Messrs.: G. A. COUNT BENTINCK, (Lepidopt.); Dr. J. G. BETREM (Hym.); Dr. H. C. BLÖTE (Hom.); FATHER CHRYSANTHUS (Aran.); P. H. v. DOESBURG Jr. (Staphyl. Carab.); F. I. v. EMDEN (Col. larvae); G. L. v. EYNDHOVEN (Aran. Acari); F. C. J. FISCHER (Trichopt.); W. H. GRAVESTEIN (Het.); Dr. L. v. d. HAMMEN (Opil.); C. A. W. JEEKEL (Diplopoda); Dr. G. KRUSEMAN (Corrod.); BROTHER Dr. THEOWALD (Dipt.); P. M. F. VERHOEFF (Hym.); P. v. d. WIEL (Col.) and Dr. J. WILCKE (Hym.) for the identifications of respective insect groups.

(c). Results

As has been emphasized by previous authors e.g. KONTKANEN (l.c.), the QS method (cf. p. 22) is decidedly preferable to the dominance affinity method, though the former has the drawback that selective species are insufficiently noticed.

The total number of species, found in the transect however, amounts to 368, which makes this matter unfit for this process. Therefore, we have eliminated a number of species which have been found once or only a few times in the investigated area (cf. table I) and which are considered to be either incidental or so rare that they are quantitatively of no value to the biocenosis, though the possibility exists that a few character species are among them.

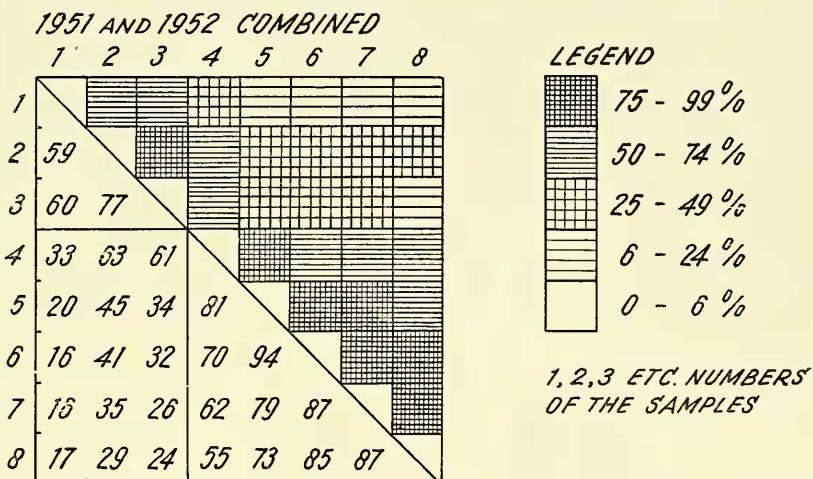
For the selection of these species we used the criterion that a species should be represented by a total of at least 10 individuals, and that it should have been collected at least once in every year of investigation.

Since the conclusion of the investigation, the main dune ridge between km-marks 18 and 20 has been severely damaged by the sea as a result of strong gales and high floods (Febr. 1953, Dec. 1954) which caused the disappearance of a considerable part (almost $\frac{1}{3}$) of the transect, so any continuation of the census in this spot has been made impossible.

The results are represented in the QS trellisdiagram (graph. 3). The faunal affinity of the first 2 samples is evident but not very strong (59%). Between the second and the third, however, it becomes stronger which is reflected in the vegetational transition, observed in sample plot no. 2 and 3 (cf. p. 17). On the other hand the affinity between samples no. 4, 5, 6, 7 and 9 proves to be clear, as are the vegetational relationships in the surveys (cf. p. 17 & 18).

It appears then, that the main dune ridge which runs between samples no. 3 & 4 separates two distinct zoocenoses: a seaward (samples no. 1, 2, 3), and a landward one (samples no. 4, 5, 6, 7, 8).

On the other hand, the phytocenoses do not show such a clear-cut limitation (at least not in this position of the yellow dune area): The *Elymeto-Ammophile-*



Graph 3. Faunal similarity of the samples, according to Sørensen's quotient of similarity method, arranged in a trellis-diagram: Results of 1951 and 1952 combined.

tum typicum shows transitions: on the seaward face of the ridge towards the *Agropyretum boreo-atlanticum* (samples no. 2—3), on the landward face towards the *E.-A. festucetosum*. Moreover, the *E.-A. typicum* extends in the transect well beyond the main dune ridge.

The frequency-density diagram is shown in graph 6a—c. As a result, the species can be classified into five groups, according to their ecological preferences (cf.: Autecology, p. 267). These groups are:

- (i) *Halobionts*, which are only found in coastal areas.
- (ii) *Halo-psammophiles*. We have established this group for those species which have a tolerance for a high salt content, but which have also been found on sandy soil elsewhere.
- (iii) *Psammophiles* which are found everywhere on sandy soil, but rarely or not in places with a high salt content.
- (iv) *Ubiquists* which are found everywhere in suitable places for animals to live.
- (v) *The social Formicidae* which have been treated separately.
- (vi) *A small number of flying insects* which are evenly distributed in the investigated area. They are good performers on the wing and move freely from one biotope into the other (either actively or passively dispersed by the wind).

These groups have been established by means of data collected during our investigations, combined with those derived from references given by authors of earlier works.

(d). Discussion

We have stated by means of the trellis-diagram that faunal affinities exist between samples nos. 1, 2, and 3 on the one hand and nos. 4, 5, 6, 7, and 8 on the other (graph 3).

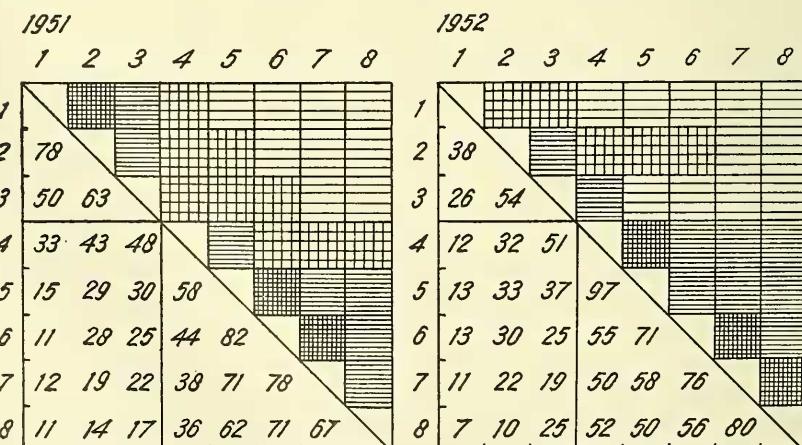
The main division between the faunal components is established by the crest:

of the main dune ridge ("zeereep"), the nos. 1, 2, and 3 being situated on the seaward- the nos. 4, 5, 6, 7 and 8 on the landward face. The exposure of the seaward face to mobile sand particles borne by onshore winds causes an environment for small animals quite different from that on the landward side of the ridge, where the wind loses much of its force and the airborne sand is shed.

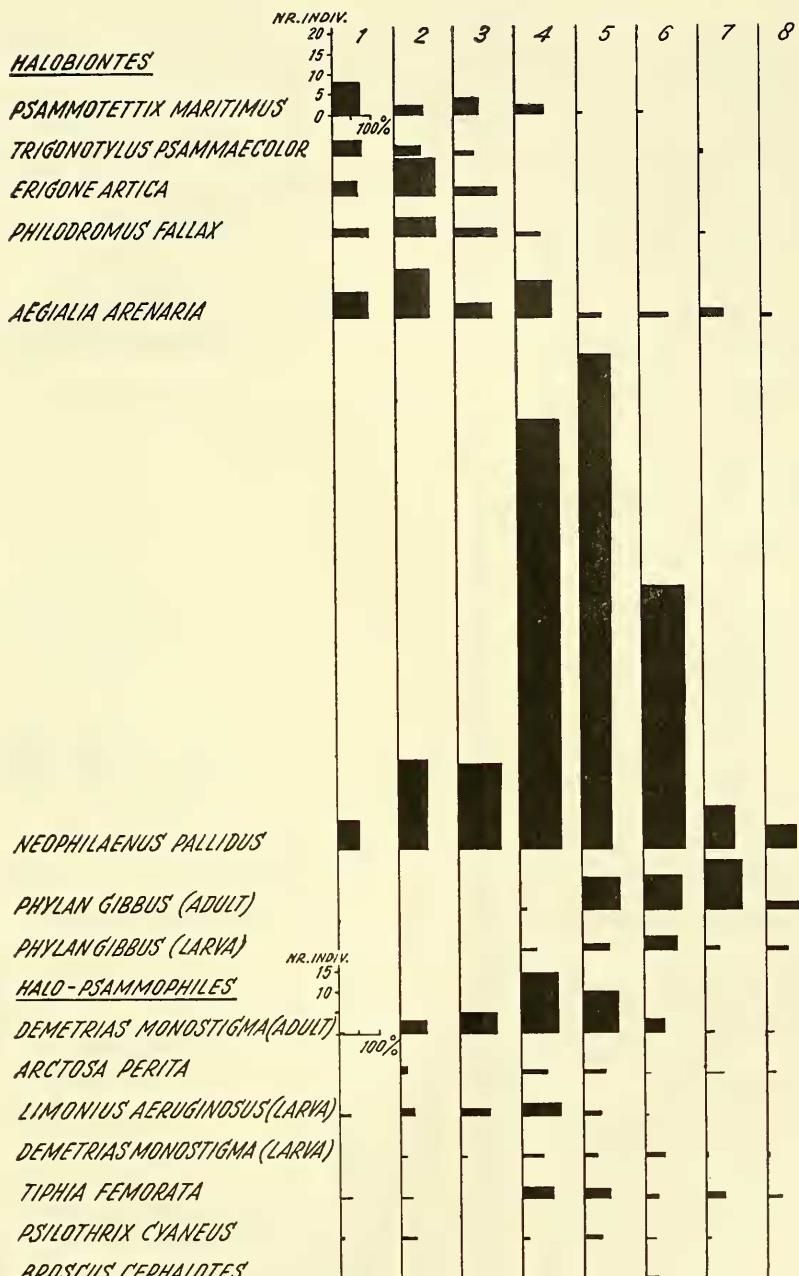
These onshore winds and shifting sands probably build up a barrier for many insects which favour the surface layers of the dune area and which are, by their constitution, liable to quick desiccation or to damage by windblown spray. The fact that the surface of the seaward dune face is always more or less mobile and that the base of the tufts of Marram grass is constantly being buried by sand (after a summer gale an addition of 30 cm (1 ft.) of sand has been observed) will be highly unfavorable to small burrowing arthropod species. The same goes for the mechanical action of the airborne sand particles. VAN DIEREN (l.c.) mentions leaves of cabbages on Terschelling which had been perforated by flying sand grains. It seems probable that insects with a weak carapace, e.g. larvae of beetles, bugs and cicadas will suffer from this cause. The small number of herbivorous arthropods living on the seaward face of the main ridge, again, renders this site unfavorable for predatory species (Carabids and Staphylinids) through lack of suitable food. The absence of leaf litter (shelter!) too, will be of importance for many small hygrophilous species.

The *Elymeto-Ammophiletum typicum*, on the contrary, thrives on a constant supply of sand, minerals (Ca, N) and organic matter from the drift line to the main dune ridge, which causes a luxuriant growth of Marram (*Ammophila arenaria*) even beyond the crest, where that part of the airborne particles which has been blown over the top, is shed. So here a slight overlap between faunal and vegetational communities comes into being. (Compare fig. 2, graph 3 and the vegetational surveys on p. 249—251).

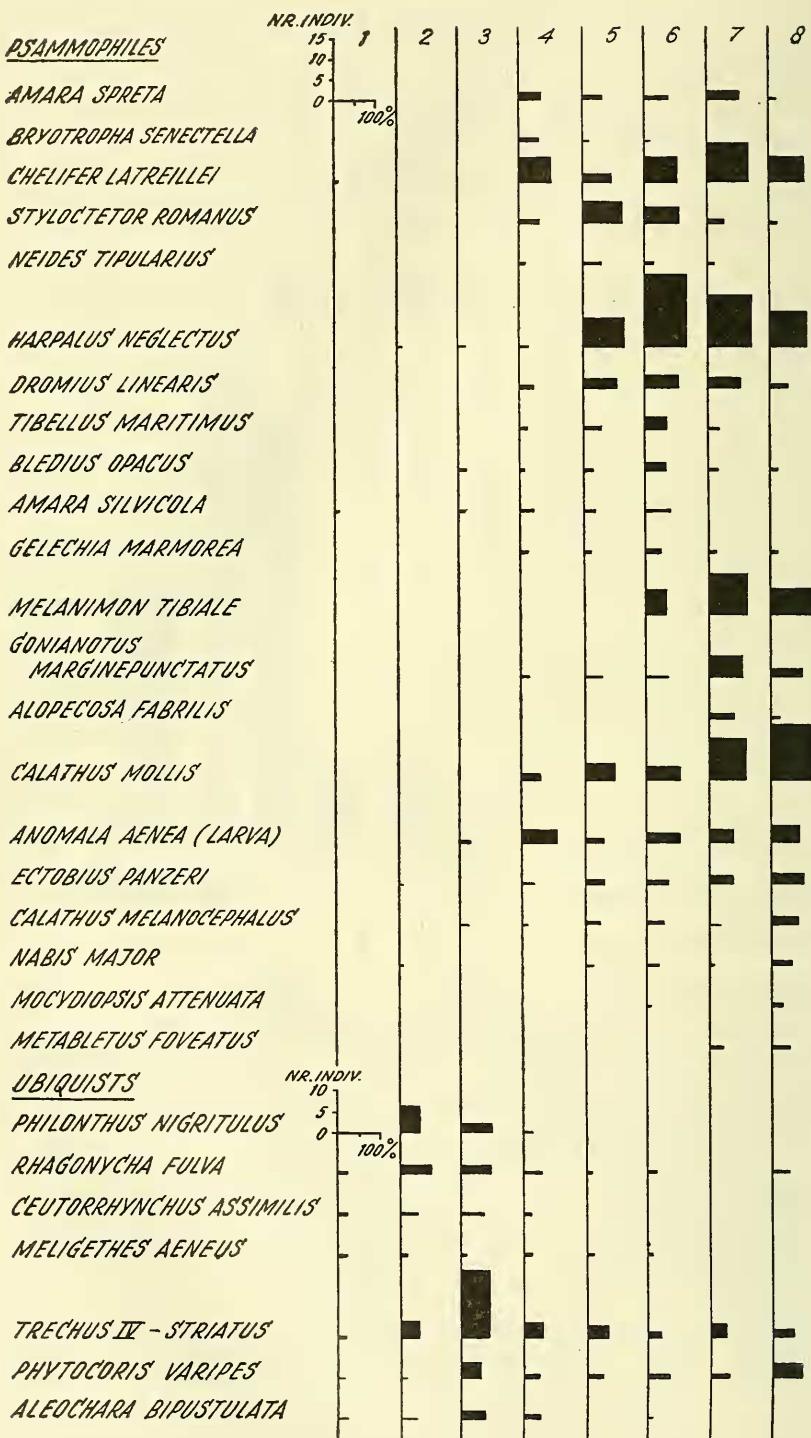
We may conclude that faunal and vegetational relations coincide for a greater part, though they are not identical, the fauna reacting quicker to leeward than the vegetation.



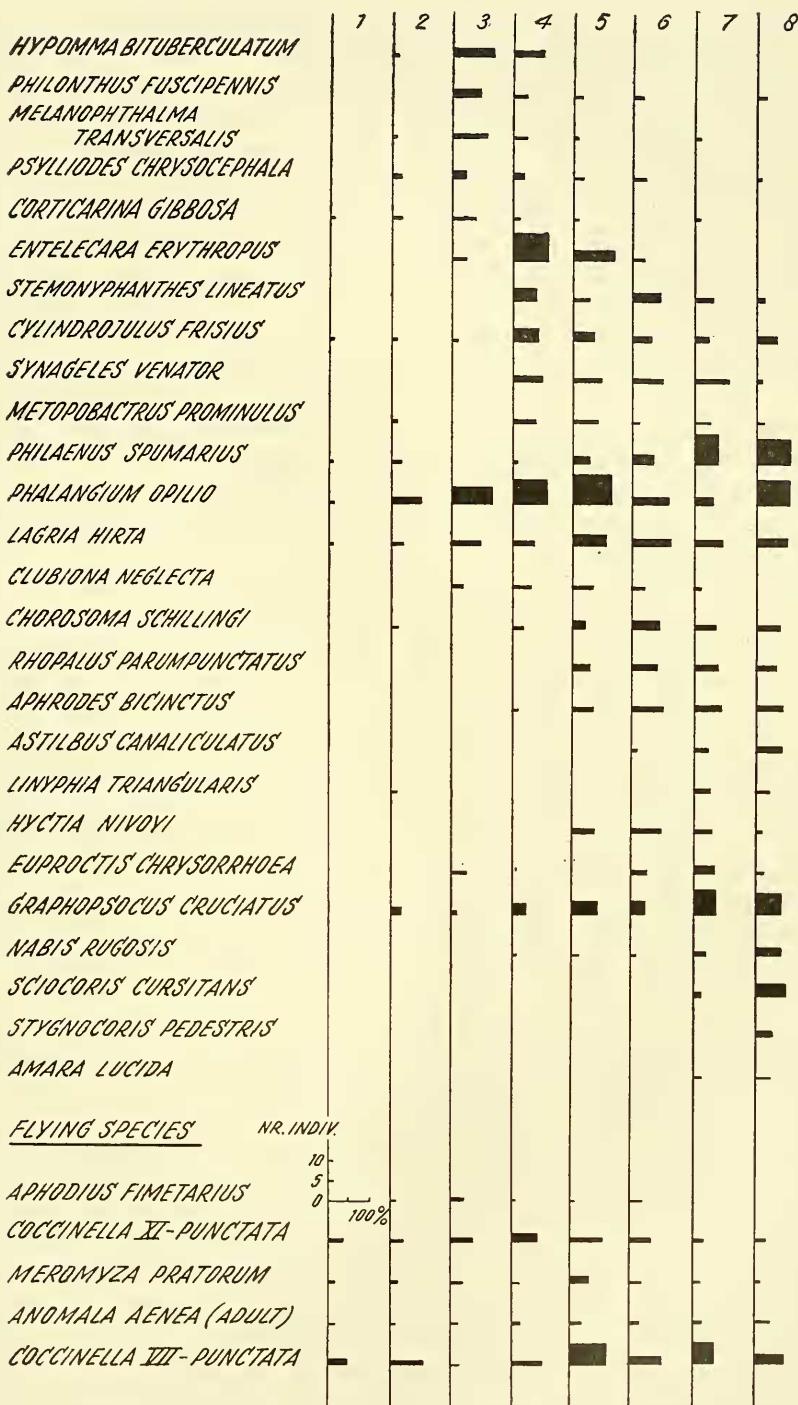
Graph 4. Faunal similarity of the samples, according to Sørensen's QS method: Results of 1951 and 1952 treated separately.



Graph 6a. Frequency-density diagram of the faunal elements in the yellow dune of Terschelling. The nrs. 1—8 correspond to the sample plot analyses of the vegetational communities. (For *Erigone artica* read *E. arctica*).



Graph 6b. Frequency-density diagram of the faunal elements in the yellow dune of Ter-schelling. The nrs. 1—8 correspond to the sample plot analyses of the vegetational communities



Graph 6c. Frequency-density diagram of the faunal elements in the yellow dune of Terschelling. The nrs. 1—8 correspond to the sample plot analyses of the vegetational communities. (For *Clubione neglecta* read *C. similis*).

When the samples of 1951 and 1952 are treated separately by the QS-method (graph 4) a difference, mainly in the first two samples, becomes evident, whereas the quotients of the sampling no.s 4, 5, 6, 7 and 8 bear a marked agreement. A number of reasons may be put forward as an explanation: (i) unfavorable weather conditions in spring which result in a retarded development of the animals (1951). (ii) offshore winds during the sampling period by which small arthropods may be blown towards the beach and distributed over the seaward (and this time leeward) face of the dunes (1951). (iii) onshore winds during the collecting period by which the animals are killed or blown inland over the crest of the main dune ridge (1952).

As a matter of fact, during the first two weeks of August, 1951, southerly offshore winds prevailed, which enabled a number of insects to settle on the seaward (= leeward) slope of the main ridge. During the same period in 1952, however, fine weather with a steady N breeze probably drove back many insects from the seaward, but this time windward, face of the ridge.

The frequency-density diagram (cf. BARNES l.c.) too, shows quite independently from the QS-diagram, the division of the sample area into two faunal communities (cf. graph 6 and table VI).

Particulars on the local character species and other groupings which have been indicated on p. 255, will be discussed on the following lines.

(i) The halobionts are an interesting group, as they are only distributed along salt and brackish waters. They can be subdivided into 3 parts: *Psammotettix maritimus*, *Trigonotylus psammaecolor*, *Erigone arctica* and *Philodromus fallax* which all reach their maximum density in the sample plots on the seaward slope, though they are also found in small numbers in a few more inland plots of the transect. Two other species, *Aegialia arenaria* and *Neophilaenus pallidus* are distributed in the entire area, but have their peak distribution past the crest of the main dune ridge in the *E.-Ammophiletum typicum* and the *E.-Ammophiletum festucetosum*. Finally, *Phylan gibbus* gives quite another picture: for although it is a true halobiont which is thought to prefer coastal regions, it is only represented in the inland area and has thus far never been collected on the seaward face of the main dune ridge (table VI, 1).

It is interesting to state that the halobionts ecologically do not make a homogeneous unity, but can be divided into two stenocous groups, one in the seaward and one in the landward part of the transect. A third group appears to be more euryecous as it is found to be distributed in the entire transect.

ii) The halo-psammophiles are represented by a small number of species which, by previous references are known to be psammophiles. This group has been created by the authors in order to make a differentiation between these species which obviously have a greater tolerance for a high salt content of the soil as they are found in considerable numbers on the exposed seaward face of the main dune ridge (though they always attain their maximum density more inland), and those psammophiles which occur abundantly in the landward part of the transect (and are only rarely met on the seaward face of the ridge). Unlike the halobionts they are found also elsewhere on sandy soil, landdunes, heaths &c.

It is a noteworthy detail that the larvae of *Demetrias monostigma* are found only in numbers across the crest of the main ridge, whereas the adults which are

Table VI. Density/16 m²

Species	Sample plot nos.							
	1	2	3	4	5	6	7	8
1. HALOBIONTS								
<i>Psammotettix maritimus</i>	8.0	1.7	4.0	2.1	0.2	0.2	—	—
<i>Trigonotylus psammaecolor</i>	3.5	2.5	0.6	—	—	—	0.1	—
<i>Erigone arctica</i>	3.4	9.0	2.0	—	0.1	—	—	—
<i>Philodromus fallax</i>	1.9	4.4	1.7	0.1	—	—	0.1	—
<i>Aegialia arenaria</i>	6.5	1.2	3.4	9.0	1.3	1.1	1.8	0.5
<i>Neophilaenus pallidus</i>	7.3	22.5	21.5	104.5	121.2	64.3	10.0	5.0
<i>Phylan gibbus</i> (ad.)	—	—	—	0.5	8.0	8.5	12.6	2.1
<i>Phylan gibbus</i> (larva)	—	—	—	0.6	1.9	3.4	1.2	3.7
2. HALO-PSAMMOPHILES								
<i>Demetrias monostigma</i>	0.1	3.0	4.7	17.6	9.9	4.1	0.7	0.1
<i>Arctosa perita</i>	—	2.6	0.3	3.9	1.9	3.7	3.8	0.7
<i>Limonius aeruginosus</i> (larva)	0.3	1.5	1.6	3.0	1.0	0.2	—	—
<i>Tiphia femorata</i>	0.3	0.6	—	3.0	2.5	1.0	1.5	0.5
<i>Demetrias monostigma</i> (larva)	—	0.2	0.4	1.3	0.9	0.5	—	—
<i>Psilotricha cyaneus</i>	0.2	0.6	—	0.2	1.3	0.4	0.1	—
<i>Broscus cephalotes</i>	0.2	0.5	0.3	0.5	0.3	0.9	0.4	—
3. PSAMMOPHILES								
<i>Amara spreta</i>	—	—	—	2.3	1.4	0.8	2.0	0.4
<i>Bryotropha senectella</i>	—	—	—	0.9	0.4	0.2	—	—
<i>Chelifer latreillei</i>	0.1	—	—	6.7	22.2	6.0	9.4	6.3
<i>Stylocetor romanus</i>	—	—	—	0.9	5.4	5.0	1.0	0.3
<i>Neides tipularius</i>	—	—	—	0.1	0.4	0.3	0.4	0.4
<i>Harpalus neglectus</i>	—	0.1	0.1	0.5	4.1	17.4	12.3	8.5
<i>Dromius linearis</i>	—	—	—	0.6	2.5	2.8	2.7	1.0
<i>Tibellus maritimus</i>	—	—	—	0.2	0.6	2.8	1.0	—
<i>Harpalus servus</i>	—	—	—	0.1	0.8	2.4	1.2	0.9
<i>Chorosoma schillingi</i>	—	0.4	—	0.4	1.9	2.2	1.4	1.1
<i>Bledius opacus</i>	—	—	—	0.1	0.2	0.5	1.8	0.2
<i>Amara silvicola</i>	0.1	—	0.1	0.3	0.3	1.6	—	—
<i>Gelechia marmorea</i>	—	—	—	0.1	0.4	0.5	0.1	0.5
<i>Melanimon tibiale</i>	—	—	—	—	—	6.8	10.0	6.4
<i>Gonianotus marginepunct.</i>	—	—	—	0.2	0.6	0.8	5.3	2.3
<i>Alopecosa fabrilis</i>	—	—	—	—	—	—	0.6	0.1
<i>Calathus mollis</i>	—	—	—	1.7	4.6	3.7	8.6	13.4
<i>Anomala aenea</i> (larva)	—	—	0.1	2.8	1.3	2.3	3.0	3.8
<i>Ectobius panzeri</i>	—	0.1	—	0.4	1.3	0.8	1.9	2.5
<i>Calathus melanocephalus</i>	—	—	0.1	0.1	1.0	1.1	0.2	2.1
<i>Nabis major</i>	—	0.1	—	—	0.4	0.3	0.6	1.4
<i>Mocydiopsis attenuata</i>	—	—	—	—	—	0.5	—	1.3
<i>Metabletes foveatus</i>	—	—	—	—	—	—	0.4	0.9
4. UBIQUISTS								
<i>Philonthus nigritulus</i>	—	6.7	2.1	0.3	0.1	0.1	—	0.1
<i>Rhagonycha fulva</i>	0.3	1.9	1.9	0.5	0.1	0.2	—	0.5
<i>Ceutorhynchus assimilis</i>	0.2	1.0	1.0	0.2	—	—	—	—
<i>Meligethes aeneus</i>	0.2	0.8	0.1	0.3	—	0.2	0.2	—
<i>Trechus IV-striatus</i>	0.4	4.0	16.4	3.4	2.9	1.3	1.1	1.9
<i>Phytocoris varipes</i>	0.1	0.1	3.9	1.1	0.8	1.0	1.0	3.5
<i>Aleochara bipustulata</i>	0.5	0.5	2.1	1.0	—	0.1	—	—

Species	Sample plot nos.							
	1	2	3	4	5	6	7	8
<i>Hypomma bituberculatum</i> . . . — 0.1 2.1 1.6 — — — —								
<i>Philonthus fuscipennis</i> . . . — — 2.0 0.4 0.2 0.2 — 0.3								
<i>Melanophthalma transversalis</i> . . — 0.8 1.9 0.6 0.1 — 0.1 —								
<i>Psylliodes chrysocephala</i> . . . — 1.4 1.7 1.5 0.7 0.4 — 0.1								
<i>Corticarina gibbosa</i> . . . 0.1 0.5 1.0 0.3 0.1 0.1 — 0.1								
<i>Entelecara erythropus</i> . . . — — 0.3 6.4 2.9 0.3 — —								
<i>Stemonyphantes lineatus</i> . . . — — — 3.3 0.6 2.2 1.0 1.0								
<i>Cylindrojulus frisius</i> . . . 0.2 0.4 0.1 3.1 2.4 1.7 1.7 1.5								
<i>Synageles venator</i> . . . — — — 1.7 1.0 1.0 1.2 1.0								
<i>Metopobactrus prominulus</i> . . . — 0.1 — 1.3 1.0 0.1 0.4 0.3								
<i>Philaenus spumarius</i> . . . 0.1 0.3 — 0.1 19.6 2.7 9.2 9.2								
<i>Phalangium opilio</i> . . . 0.4 2.4 3.3 6.4 7.7 2.3 2.0 6.3								
<i>Lagria hirta</i> . . . 0.1 0.5 1.3 1.3 2.5 1.5 1.8 1.9								
<i>Clubiona similis</i> . . . — — 0.7 0.7 1.0 0.3 0.2 —								
<i>Rhopalus parumpunctatus</i> . . . — — — — 1.5 1.7 1.7 1.4								
<i>Aphrodes bicinctus</i> . . . — — — — 0.1 1.2 1.6 1.6								
<i>Calathus erratus</i> . . . — 0.2 0.1 1.7 3.5 9.2 10.2 5.1								
<i>Astilbus canaliculatus</i> . . . — — — — — 0.4 1.8 1.5								
<i>Hyctia nivoyi</i> . . . — — — — — 1.0 1.1 1.4 0.3								
<i>Euprotocis chrysorrhoea</i> . . . — — 0.1 — — 0.5 1.3 0.1								
<i>Graphopsocus cruciatus</i> . . . — 2.0 1.3 3.0 4.5 3.5 6.6 7.9								
<i>Nabis rugosus</i> . . . — — — 0.1 0.6 0.4 1.4 3.0								
<i>Sciocoris cursitans</i> . . . — — — — — — 1.0 2.9								
<i>Stygnocoris pedestris</i> . . . — — — — — — — 1.5								
<i>Amara lucida</i> . . . — — — — — — — 0.6 0.9								

5. SOCIAL HYMENOPTERES

number of colonies/16 m²

<i>Tetramorium caespitum</i> . . . — — — — — — 3.3 0.6 1.2								
<i>Myrmica scabrinodes-group</i>								
(M. sabuleti, M. puerilis and M. puerilis var. dolens) . . . — — — — — — 0.1 0.6 1.8								
<i>Lasius niger</i> . . . — — — — — — — 0.1? 0.6								

6. FLYING SPECIES

<i>Aphodius fimetarius</i> . . . — 0.2 0.6 0.1 0.1 0.1 0.2 —								
<i>Coccinella XI-punctata</i> . . . 1.0 0.5 1.0 2.2 1.2 0.8 0.7 0.3								
<i>Anomala aenea</i> (ad.) . . . 0.2 0.1 0.1 0.3 0.5 0.3 0.2 0.4								
<i>Meromyza pratorum</i> . . . 0.2 0.2 0.4 0.4 1.5 0.3 0.2 0.1								
<i>Coccinella VII-punctata</i> . . . 1.5 1.4 — 0.8 4.6 2.2 5.2 2.5								

more mobile, have been collected on the seaward face also (cf. table VI, 2).

(iii) The p s a m m o p h i l e s are a group which avoids places with a high salt content, as is clearly shown by their distribution. They can be found everywhere in sandy regions, landdunes and heaths. Their peak abundance is always in the inland sections of the transect and their presence on the seaward slope of the dune ridges is considered to be incidental (table VI, 3).

(iv) The ubiq u i s t s are represented by a rather miscellaneous group of arthropods, a number of which is evenly distributed in the entire transect (eg. *Trechus IV-striatus*, *Phalangium opilio*, *Cylindrojulus frisius* and *Lagria hirta*), though they all show only small numbers in the fore-dunes (*Agropyretum boreo-atlan-*

ticum). Others are more or less scattered over the investigated area, and others again have their peak abundance in the more inland region of the transect. We have the impression that their presence is mostly incidental. It proves moreover that those species which are usually called "ubiquists" are by no means a homogeneous group. On the contrary, they show marked differences in tolerance of salt content and climatic conditions (cf. table VI, 4).

(v) We must treat the Ants (social Formicidae) as a separate group as it proved impossible to collect the complete content of the nests which were found within the sampling areas.

Dr. K. U. KRAMER, who made the identifications of the ants, makes the following comment:

The low species content of the yellow dunes is an interesting feature. Only 3 species have been found thus far: *Tetramorium caespitum*, a typical psammophile; *Lasius niger*, an ubiquist, and 3 subspecies (or closely related species) of the *Myrmica scabrinodis* group: *M. sabuleti* Meinert, *M. puerilis* Stärcke and *M. puerilis* var. *dolens* Stärcke, which can only be identified by their males. Dealate ♀♀ of *Tetramorium* have been found in sample plots nos. 2, 3, 4, 5, and 7, but no alatae were found, as in *Myrmica scabrinodis*. This is easily understood as the copulation flight of the former takes place about a fortnight earlier as in the latter. A very big number of *Lasius* ♀♀ (alate and dealate) is quite incidental, as swarming in this species usually coincides with the period of investigation (table VII).

Table VII. Occurrence of ants

Phytocenological characterization	<i>Agrop. bor. -atl.</i>	Sample plot nos.						<i>Hipp. phase Tort. Phlet.</i>
		1	2	3	4	5	6	
<i>Tetramorium caespitum</i>	♀ deal.	—	2	2	1	94	28	13
	♀	—	—	—	—	—	18	21
<i>Lasius niger niger</i>	♀ al.	—	—	—	—	—	—	—
	♀ deal.	—	249	92	122	42	48	7
	♀	—	—	—	—	—	—	2
	♂	—	7	2	—	—	—	—
<i>Myrmica scabrinodis</i>	♀ al.	—	7	—	—	2	13	27
Three species combined, owing to absence of males	♀ deal.	—	—	5	8	10	9	12
	♀	—	—	—	—	1	103	89
<i>Myrmica sabuleti</i>	♂	—	—	1	—	—	2	11
<i>Myrmica puerilis</i>	♂	—	—	—	—	—	—	8
<i>Myrmica puer. var. dolens</i>	♂	—	—	1	—	—	—	6
<i>Myrmica scabrinodis</i> group males not identified	—	—	6	—	—	—	—	—
<i>Myrmica laevinodis</i>	♀ deal.	—	—	—	—	—	—	1

The workers of *Tetramorium* are found in sample plots nos. 6, 7, and 8, so well past the main dune ridge. In this region the flying sand particles have been shed and the colonies are not liable to be covered by the shifting sands. The same goes for the colonies of the *Myrmica scabrinodis* group (cf. table VIIa).

Comparing the distribution of the colonies of *T. caespitum* and of the *M.*

scabrinodis group, it is remarkable that the former species has its peak in sample plot no. 6 (*E.-Ammophiletum festucetosum*), the latter in no. 8 (*Hippophaë* phase of the *Tortuleto-Phleetum*). This indicates, in our opinion, that *T. caespitum*, being a psammophile, prefers the more open, drier vegetation of Marram Grass, unlike *M. scabrinodis*, which prefers the denser vegetation of the *Hippophaë* phase (table VIII).

Table VIII. Abundance of ant colonies.

Phytocenological characterization		<i>Agopyr. Bor.-Atl.</i>	<i>E.-Ammoph. typicum</i>	<i>E.-Ammoph. festuc.</i>	<i>Hippophae phase</i>
Sample plot nos.		1 2	3 4	5 6	7 8
<i>Tetramorium caespitum</i>	1950			11	1? 3
	1951			12	3 3
	tot.			23	4 3
<i>Lasius niger</i>	1950				1? 3
	1951				
	tot.				1? 3
<i>Myrmica scabrinodes</i> gr. (<i>M. sabuleti</i> , <i>M. puerilis</i> , <i>M. puerilis</i> var. <i>dolens</i>)	1950			1	3 3
	1951			—	1 6
	tot.			1	4 9

1952 not investigated.

Lasius workers have only been found in sample plots no. 7 and 8. Whether a colony of this ubiquitous species existed in sample plot no. 7 is not certain. It is certain that 3 colonies were found in no. 8.

The total absence of *Myrmica ruginodis* and *M. laevinodis* is notable.

(vi) The last group, a small number of species, all good performers on the wing which are not tied to a particular region. As a rule they move freely in the entire transect, unhampered by terrestrial boundaries. Their only peril is to be seized by an offshore wind and taken out to sea. Their presence in any part of the transect is occasional, e.g., in *Aphodius* spec. and *Coccinella VII-punctata*. Others are found, because they are halobionts (*C.XI-punctata*, *Meromyza pratorum*) or because they are psammophiles (*Anomala aenea*). No definite conclusion concerning their distribution can be drawn from these data, for we are certain, that only a small part of the total population has been captured, our method of sampling being unfit for quantitative collection of these flyers (table VI, 6).

The collected data enable us now to characterize the biocenoses which have been established in the previous pages (cf. table IX).

5. Summary

a) An extensive 3-year survey (zoological, botanical, and microclimatological) of the coastal dune region in the nature reserve "Boschplaat" on Terschelling (West Frisian Isles) has been made by means of a quantitative sampling method (table I).

Table IX. Characterization of the biocenoses

Seaward community <i>Agropyretum b.a.</i> and <i>E. Amm. typicum</i>	Landward community <i>E. Amm. festucetosum</i> and <i>Hippophaë-phase</i>
Local character species:	Local character species:
1. <i>Psammotettix maritimus</i> 2. <i>Trigonotylus psammaecolor</i> 3. <i>Erigone arctica</i> 4. <i>Pholidromus fallax</i>	1. <i>Phylan gibbus</i>
Differential halobionts:	
1. <i>Aegilia arenaria</i> 2. <i>Neophilaenus pallidus</i>	
Differential halo-psammophiles	
1. <i>Demetrias monostigma</i> 2. <i>Arctosa perita</i> 3. <i>Limonius aeruginosus</i> 4. <i>Broscus cephalotes</i> 5. <i>Psilotrichus cyaneus</i> 6. <i>Tiphia femorata</i>	
Accessory species:	Accessory species:
none	1. <i>Amara spreta</i> 2. <i>Bryotropha senectella</i> 3. <i>Chelifer latreillei</i> 4. <i>Styloctetor romanus</i> 5. <i>Neides tipularius</i> 6. <i>Harpalus neglectus</i> 7. <i>Dromius linearis</i> 8. <i>Tibellus maritimus</i> 9. <i>Bledius opacus</i> 10. <i>Gelechia marmorea</i> 11. <i>Amara silvicola</i> 12. <i>Melanimon tibiale</i> 13. <i>Gonianotus marginepunct.</i> 14. <i>Alopecosa fabrilis</i> 15. <i>Anomala aenea</i> (larva) 16. <i>Calathus mollis</i> 17. <i>Ectobius panzeri</i> 18. <i>Nabis major</i> 19. <i>Mocydiopsis attenuata</i> 20. <i>Metabletus foveatus</i>

b) The faunal and vegetational communities agree, though they are not quite identical (cf. p. 32). According to the quotient of similarity, the animals can be grouped into two communities: a seaward and a landward one (cf. table VI & VIII).

c) The distribution of the vegetation depends on the supply of airborne sand particles and organic matter from the shore and the drift line, whereas the animals probably are mainly affected by various influences: (i) mechanical damage by flying sand particles; (ii) physical injury by desiccation and salt content of onshore wind; (iii) ecological maladaptation by absence of protective leaf litter and in case of predators, of suitable food. The *E.-Ammophiletum* extends well beyond the main dune ridge (though the growth of Marram is less luxuriant there) because part of the flying sand is shed in that region. For the animals, the main dune ridge is the principal boundary, as only few species probably can stand the adverse circumstances on the seaward face of this ridge (cf. table VI & VIII).

d) The so-called halobionts are to be divided in three separate groups: (i) species, living principally on the seaward face of the main ridge. (ii) species which are more or less equally distributed over the entire yellow dune area and (iii) a species which is found in the landward part of the transect only.

e) A small group of halo-psammophiles (for a definition cf. p. 260) is distributed in the seaward- as well in the landward part of the yellow dune region, but these species never attain their maximal abundance on the seaward slope and they are also found in sandy regions far inland. (cf. table VI).

f) The psammophiles proper are only found occasionally on the seaward slope. Their main distribution is always in the more inland region (cf. table VI).

g) The colonies of ants (social Formicidae) are only found in the sample plots nos. 6, 7 and 8, as these are probably particularly sensitive to being covered by airborne sand particles. Winged and unwinged males and females may be found during the mating season everywhere along the transect: their presence is purely incidental (cf. table VIII).

h) The ubiquists are a heterogenous group. The species may reach their maximal abundance in any of the 8 sampling areas of the transect and their distribution is probably mostly incidental (cf. table VI).

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III. AUTECOLOGY

1. Introduction.

In the following section those species which were represented by more than 10 individuals in the samples will be discussed in detail. We have tried to elucidate the circumstances under which a certain species thrives.

From these data, derived from earlier publications, the ecological characteristics of the species have been carefully checked against their presence in the biotopes investigated. These data have been assimilated in graph 6a—c, tables VI and VIII.

2. Autecological data.

1. *Psammotettix maritimus* Perr. (Hom. Jassidae). On *Ammophila arenaria* from Calais to the East-Frisian Isles (HAUPT). A typical halobiont, abundant in the *Agropyretum boreo-atlanticum*.

2. *Trigonotylus psammaecolor* Reutt. (Heteropt. Miridae). In the dunes on *Elymus* and *Ammophila* (RECLAIRE). Abundant in the *Agropyretum* and in the *Elymeto-Ammophiletum typicum*; less frequent in the *E.-Ammophiletum festucetosum*.

3. *Erigone arctica* (White). (Aran. Linyphiidae). "On the sides of tidal estuaries and on the seashore, amongst stones and seaweed". (LOCKET & MILLIDGE). Abundant on the seaward slope of the main dune ridge, in the *Agropyretum* and the *E.-Ammophiletum typicum*.

4. *Philodromus fallax* Snd. (Aran. Thomisidae). "...it is found only in sandy places, particularly on sand-dunes on the coast" (LOCKET & MILLIDGE). Abundant on the seaward slope of the main dune ridge but less than *Erigone arctica*.

5. *Aegialia arenaria* F. (Col. Scarabaeidae). Common in the seaward dune range (EVERTS). A typical halobiont beetle, abundant in the entire transect, though less so in the *Hippophaë* phase of the *Tortuleto-Phleetum*.

6. *Neophilaenus pallidus* Hpt. (= *Neophilaenus lineatus* L. f. *pallida* Hpt, only recently made a true species by HAUPT) (Hom. Cercopidae). Borkum, coast of the North Sea (HAUPT). Extremely abundant leafhopper (max. density 121.2 per 16 m²) in the *Elymeto-Ammophiletum typicum* and the *E.-A. festucetosum*, less so in the *Agropyretum boreo-atl.* and in the *Hippophaë* phase.

7. *Phylan gibbus* F. (Col. Tenebrionidae). On the coast of the North and Baltic Sea on salt containing sandy soil (REITTER). True halobiont but only found in the *E.-Ammophiletum festucetosum* and in the *Hippophaë* phase, on the landward side of the main dune ridge.

8. *Demetrias monostigma* Sam. (Col. Carabidae). Common, especially in the dunes among the *Ammophila* stems (EVERTS). Occurs frequently along humid banks of brooks and marshes, between reeds &c; also frequent in the dunes under tussocks of *Ammophila* and *Elymus* (BURMEISTER). Halo-psammophile, fairly common throughout the entire transect, except the *Hippophaë* phase, but more abundant on the landward face of the main ridge.

9. *Arctosa perita* (Latr.). (Aran. Lycosidae). Common in sandy places along the coastline, but also found near rivers and lakes inland, on downs and heaths (DAHL). "Frequent on dry heaths and sandy places, where it is found running about in the sunshine" (LOCKET & MILLIDGE). Halo-psammophile, fairly abundant, but absent in sample plot no. 1.

10. *Limonius aeruginosus* Oliv. (Col. Elateridae). Very common in dry, sandy regions, especially in the dunes (EVERTS). Halo-psammophile, collected only as a larva, as the adults occur in spring. Fairly abundant, but absent in the *Hippophaë* phase.

11. *Tiphia femorata* F. (Hym. Tiphiidae). Cumbersome performer on the wing, parasitic on *Anomala aenea* larvae (BENNO). Common in sandy regions (OUDEMANS). Halo-psammophile, fairly common in the entire transect, but more abundant in the inland part.

12. *Psilotrix cyaneus* Oliv. (Col. Cantharidae). Not rare from May to August in the dunes on flowering *Hieracium*, *Leontodon*, *Sonchus* and other yellow Composites (EVERTS). In the Western part of Germany, Westfalen, Hamburg, Norderney, Borkum and Heligoland (REITTER). In small numbers on the Compositae in the landward part of the transect, but also a few individuals on the seaward face of the main dune ridge, probably dispersed by the wind.

13. *Broscus cephalotes* L. (Col. Carabidae). Common on sandy soil, in dunes and heaths, living in tunnels under stones, often two individuals together (δ and φ) but each in a separate tunnel, watching for prey (EVERTS). This species is very abundant on the Frisian Isles in the *Elymus*-zone, where it lives on Amphipods (MROZEK-DAHL). This big carabid beetle is evenly distributed in small numbers, each individual probably occupying a separate territory. On Terschelling it prefers the more landward regions, but has been found occasionally in the *Agropyretum boreo-atlanticum*.

14. *Amara spreta* Dej. (Col. Carabidae). Common, especially on sandy soil (EVERTS). Psammophile beetle. Two generations with imagines from IV—V and IX—X. Small numbers have been found in the landward part of the main dune ridge only.

15. *Bryotropha senectella* Zell. (Lep. Gelechiidae). Common in the dune region of Holland, on sandy soils and heaths, a small unobtrusive moth (SNELLEN). Psammophile. In small numbers only among the *Ammophila* tufts.

16. *Chelifer latreillei* Leach. (Pseudoscorpiones = Chelonethi). Living in low walls and dunes, under stones near the coast (BROMER). Psammophile, abundant in the landward part of the transect, often in leafsheaths of dry, dead tufts of Marram.

17. *Styloctetor romanus* Cbr. (Aran. Linyphiidae). "On sandhills on the coast" (LOCKET & MILLIDGE). "Commun dans les friches sèches" (SIMON). Rare psammophile spider, in the landward part of the transect only.

18. *Neides tipularius* L. (Het. Neidae). Generally distributed on sandy soils (RECLAIRE). This bug has been found in the landward part of the transect only.

19. *Harpalus neglectus* Dej. (Col. Carabidae). A psammophile beetle, living in sandy soil, but mainly in the dunes (EVERTS). According to BURMEISTER in England and France exclusively in the dune area. *Harpalus neglectus* is the most abundant coleopteron in the dunes in August (more than 400 exs., maximal density 17.4 per 16 m²) in the transition between *E.-Ammophiletum festucetosum* and the *Hippophaë* phase of the *Tortuleto-Phleetum*. This carabid has one generation annually, adults are found from May to August.

20. *Dromius linearis* Ol. (Col. Carabidae). Common psammophile living in *Elymus arenarius* (MROZEK-DAHL). According to EVERTS in *Ammophila arenaria*. One generation annually: the larvae are developing during winter. Collected in small numbers in the landward part of the transect only.

21. *Tibellus maritimus* Menge. (Aran. Thomisidae). "On coarse grasses, rushes &c., on sandhills and rough ground" (LOCKET & MILLIDGE). Adults in summer. In small numbers in the *E.-Ammophiletum*.

22. *Harpalus servus* Dfts. (Col. Carabidae). Very common on sandy soils, especially in the dunes under stones (EVERTS). Collected in the landward part of the transect only.

23. *Chorosoma schillingi* Schill. (Het. Coreidae). A very long, slender bug, common on heather and in the dunes in August (RECLAIRE). With a few exceptions, in the landward part of the transect only.

24. *Bledius opacus* Bl. (Col. Staphylinidae). Common psammophile staphylinid, along pools in the dunes, and in wet sandy pits and along river banks. Flying about in the evening. (EVERTS). In small numbers in the *Elymeto-Ammophiletum* and in the *Hippophaë* phase.

25. *Amara silvicola* Zimm. (Col. Carabidae). Lives mainly in the sanddunes on the North- and Baltic sea coast, but also on sandy heaths, between roots and in clearings under stones (BURMEISTER). Lives in the dunes, especially in the moving dunes, but also inland between grasses and tussocks of Marram (MROZEK-DAHL). This psammophile beetle lives in small numbers in the *E.-Ammophiletum*, especially in the litter of semi-desintegrated tufts of Marram grass.

26. *Gelechia marmorea* Han. (Lep. Gelechiidae). Common in the dunes of Holland; also, but rarely, found in sandy spots and heaths (SNELLEN). A psammophile microlepidopteron, collected in the landward part of the transect only.

27. *Melanion tibiale* Seidl. (Col. Tenebrionidae). Common in the dunes, where they have been observed in large numbers on the bare sand. Sometimes noxious in plantations of pine, eating the roots of young trees. Also found in heaths (EVERTS). A psammophile beetle, fairly numerous in sample plots no.s 6, 7 and 8.

28. *Gonianotus marginepunctatus* Wlff. (Het. Lygaeidae). Reported on dry sandy soils under low vegetation (RECLAIRE). A psammophilous bug, collected in relatively small numbers in the entire landward part of the transect.
29. *Alopecosa* (= *Tarentula*) *fabilis* (Clerck). (Aran. Lycosidae). Living in open, sandy, thinly grown places in the dunes, on heaths and in pinewoods (DAHL). A typical psammophile lycosid spider, collected on Terschelling in the *Hippophaë* phase only.
30. *Calathus mollis* Marsh. (Col. Carabidae). Lives in dry sandy spots under stones (EVERTS). "On coastal dunes in Anglesey, adults emerge in Sept.-early Oct., egg-laying during Aug.-Febr." (OWEN GILBERT). Psammophile, in the landward part of the transect only.
31. *Anomala aenea* Sam. (Col. Scarabaeidae). Common in June and July, mainly in the dunes and heaths, on various shrubs and herbaceous plants, but also on alder, willow, and pine (EVERTS). Psammophile, larvae collected, with a few exceptions, only behind the main dune ridge; the adults, being good performers on the wing, occurring everywhere in the transect.
32. *Ectobius panzeri* Steph. (Blatt. Blattidae). Living in the coastal region (Belgium, Holland, S. England) or on denuded hills, but also in beech and pine forests (ZACHER). In clearings in dry woods, on herbaceous plants and in heaths, common in the N of France (CHOPARD). A small cockroach, with one exception, always in the landward part of the transect.
33. *Calathus melanocephalus* L. (Col. Carabidae). Very common under stones on sandy soils (EVERTS). "*C. melanocephalus* adults have their peak during IX and early X. Egg laying occurs during VIII—II with a peak in autumn. Larvae of all three instars are found in winter" (OWEN GILBERT). The small numbers of this common species in the landward part of the transect may indicate a main distribution in the more inland regions.
34. *Nabis major* Costa. (Het. Nabidae). Widely distributed psammophile (RECLAIRE). With few exceptions in the *E.-Ammophiletum festucetosum* and the *Hippophaë* phase only.
35. *Mocydiopsis* (= *Thamnotettix*) *attenuata* Germ. (Hom. Jassidae). Living in sandy regions (RIBAUT). Perhaps a littoral species, with the Isle of Borkum as its northern-most boundary (GRAVESTEIN). Collected in the landward part of the transect only.
36. *Metabletus foveatus* Fourcr. (Col. Carabidae). According to MROZEK-DAHL a calcifugous beetle ("ein Boden mit geringerem Kalkgehalt wird bereits gemieden"). Common in sandy spots, e.g. in the dunes under Marram grass and dry leaves (EVERTS). As a consequence it has been collected in the more inland region which is poor in lime i.e. in the *Hippophaë*-phase of the *Tortuleto-Phleum*.

37. *Philonthus nigritulus* Grav. (Col. Staphylinidae). Common under stones, under leaves, in litter, mosses, on dungheaps, often flying about (EVERTS). The presence of this species in the transect is probably purely incidental, due to human faeces in one of the sample plots.

38. *Ceutorhynchus assimilis* Payk. (Col. Curculionidae). A common curculionid on Cruciferes (EVERTS, REITTER). Cenoxene, probably dispersed by the wind from more inland regions.

39. *Meligethes aeneus* F. (= *brassicae* Scop.). (Col. Nitidulidae). A small beetle (1.5—2 mm). Lives on flowering plants, mainly on Cruciferes, but also on *Taraxacum* and other Composites, on *Epilobium* and other plants. On warm, sunny days they have been observed flying from flower to flower. Ubiquitous (EVERTS). Probably dispersed along the transect by the wind.

40. *Trechus IV-striatus* Schrk. (Col. Carabidae). Very ubiquitous species, but even so attached to leaf litter or drift (MROZEK-DAHL). Common everywhere (EVERTS). In large numbers throughout the entire transect, but especially where the Marram grass grows abundantly (cf. sample plot no. 3).

41. *Phytocoris varipes* Boh. (Het. Miridae). Very common everywhere, mainly in low vegetation, but also in shrubs and trees (RECLAIRE). Common in the entire transect.

42. *Aleochara bipustulata* L. (Col. Staphylinidae). Very common in human excrement, also in rotting mushrooms and under fallen leaves (EVERTS). In small numbers in the seaward part of the transect. Its presence is probably purely incidental.

43. *Hypomma bituberculatum* (Wider). (Aran. Linyphiidae). A small spider, living in damp woods, on grasses and shrubs; common and locally abundant (SIMON, LOCKET & MILLIDGE). Rare in sample plots nos 2, 3 & 4.

44. *Philonthus fuscipennis* Mnnh. (Col. Staphylinidae). One of the most common staphylinids in leaf litter, under stones, in different kinds of waste, in drift, rotting mushrooms &c., often flying about (EVERTS). An ubiquitous species, collected nearly everywhere in the transect, though lacking in the *Agropyretum boreo-atlanticum*.

45. *Melanophthalma* (= *Corticarina transversalis* Gylh. (Col. Lathridiidae). Fairly common in leaf litter, dead reeds and grasses (EVERTS). Probably dispersed by the wind.

46. *Psylliodes chrysocephala* L. (Col. Chrysomelidae). Common on all species of Cruciferes (June to Sept.) (EVERTS). Probably dispersed by the wind.

47. *Corticarina gibbosa* Hrbst. (Col. Lathridiidae). Common in leaf litter and

rotting herbaceous matter (EVERTS). Probably dispersed by the wind in nearly the entire transect, excepted sample plot no. 7.

48. *Entelecara erythropus* Wstr. (Aran. Linyphiidae). "Widespread but uncommon, adults in summer" (LOCKET & MILLIDGE). In our transect in the *E.-Ammophiletum* only.

49. *Stemonyphantes lineatus* (L.) (Aran. Linyphiidae). "In a variety of situations, e.g. in rough grass, heather, bracken, on sandhills, generally common" (LOCKET & MILLIDGE). Common on damp meadows and in moors (SIMON). Adults in summer and fall. Only found in the landward part of the transect.

50. *Cylindrojulus frisius* (Verhoeff) = *latestriatus* (Curtiss) (Diplopoda, Julidae). A common species in deciduous woods on dry or boggy soil, also in the dunes (VAN EYNDHOVEN in litt.). Throughout the entire transect, but more numerous in the landward part.

51. *Synageles venator* (Lucas). (Aran. Salticidae). "This is a very rare spider, which has been taken only on a few sandhills around the coasts and in a fen. Adults in spring to summer. It is very ant-like in appearance" (LOCKET & MILLIDGE). Collected in the landward part of the transect only.

52. *Metopobactrus prominulus* (Cambr.). (Aran. Linyphiidae). "In moss, undergrowth &c., uncommon, but frequent locally, adults in spring, summer and autumn" (LOCKET & MILLIDGE). With few exceptions in the landward part of the transect only.

53. *Philaenus spumarius* L. (Hom. Cercopidae). An extremely ubiquitous leaf-hopper which is common throughout Europe on fields and grasslands (HAUPT). Mainly occurring behind the first range of dunes, but in smaller numbers in the seaward part also.

54. *Phalangium opilio* L. (Opiliones Phalangidae). A very common harvest spider with a wide distribution in fields, gardens and parks, but absent in big woods (VAN DER HAMMEN in litt.). Found throughout the entire transect, but more numerous in the inland part.

55. *Lagria hirta* L. (Col. Lagriidae). Common beetle on flowering plants and on shrubs (EVERTS). An ubiquitous species, found everywhere in the entire transect, but more numerous in the inland part.

56. *Clubiona similis* (L. Koch). (Aran. Clubionidae). Common, but not numerous, in damp fields and on trees and shrubs, also on dunes near the coast (Father CHRYSANTHUS in litt.). Living mainly in the *E.-Ammophiletum*.

57. *Rhopalus* (= *Corizus*) *parumpunctatus* Schill. (Het. Coreidae). Living in large numbers on low plants in dry fields (RECLAIRE). Collected in the landward part of the transect only.